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THE FORAGING OF ANTS

By D. M. VOWLES
Department of Psychology, Reading

The behaviour of the social insects has often been cited as one of the supreme examples of instinctive activity. It has not always been clear however in what sense the term "instinct" has been used, for this concept has had a notoriously chequered history. Recent ethological work, summarised by Tinbergen (1951), has provided a classification of behaviour which lends itself to analytical studies; and it has therefore seemed valuable to enquire how far the current ethological analysis of instinct can be applied to the social insects.

The vast literature on all aspects of social behaviour makes it necessary for a short review to be highly selective both of subject and of the work surveyed. The object of this paper is therefore not to provide a comprehensive survey of the behaviour of social insects (which is already available, for example, in Wheeler, 1924, 1928, and Schneirla, 1953) but to consider in detail the single topic of the foraging behaviour of ants, as an example of an instinctive activity. The close co-ordination of all activities within an ant colony makes such a selection artificial in the extreme, but the necessity for preliminary analytical approach is self-evident, and by treating the subject in isolation some of the problems involved become more clearly defined.

The behaviour of a forager is roughly as follows: the ant leaves the nest and searches in a more or less random manner for food (appetitive behaviour), collects the food either by drinking or by grasping it in its jaws, searches in a more or less random manner for the nest (appetitive behaviour), and distributes the food in the nest by regurgitation or by depositing solid booty among its nestmates. Each of the activities in this behavioural sequence would be expected (in the ethological view) to involve specific patterns of movement, each released by particular and specific stimuli and guided by the same or other stimuli. It is proposed here to consider if the observations on ant behaviour can be analysed in this way.

The Motivation of Foraging

Wheeler (1928) has pointed out that the foraging of ants is a response to colony hunger. This deceptively simple statement covers a complex situation, for within any colony there may be at least three hunger-sources to stimulate a prospective forager—the brood, the other adults of the colony, and the forager's own viscera. If these hunger-sources can activate different behaviour mechanisms then any forager could be motivated in any one of the three corresponding ways. It is therefore relevant to enquire if the supply of food to the three hunger-sources does involve different behavioural mechanisms.

The main criterion to resolve this problem must be the behaviour of the ant in response to stimuli from the three hunger-sources: if this behaviour is qualitatively different in the three cases one might be justified in postulating three different behavioural mechanisms; while if it is only quantitatively different this would imply the use of a single mechanism activated at different intensities by the different stimuli. Both these alternatives would seem to exist in ants.

In the Army Ants, *Eciton* sp. (Schneirla, 1933-54) and the primitive ponerines *Odontomachus* and *Euponera* (Haskins & Enzmann, 1938), which are entirely carnivorous, and show no regurgitation, the workers forage and bring home insect booty to the bivouac or nest. The pattern of behaviour is not changed by the presence of larvae or callows, but the intensity of foraging is increased in response to these immature forms. It seems that only one behavioural mechanism is used in these species independently of the goal of the activity.

In the equally primitive ponerines *Myrmecia* and *Promyrmecia*, however, (Haskins & Haskins, 1950) the situation is quite different. The adults are almost entirely nectivorous, while the larvae are carnivorous. When only eggs or pupae are present each worker forages individually and sporadically, collecting nectar for itself alone: the appearance of larvae causes an immediate change in behaviour; the workers bring back a steady stream of insect booty to the nest, and distribute it to the larvae. It seems that two different behavioural mechanisms are used, although even here (Haskins &

Whelden, 1954, and Le Masne, 1952) some regurgitation between adults and larvae does occur: there is no evidence, however, that the larvae either stimulate nectivorous foraging or solicit regurgitated nectar.

In species with a mixed diet, such as *Myrmica rubra* (personal observation) the situation seems to be intermediate, for the presence of larvae causes an increase in all foraging activity, but the foragers collect a greater proportion of protein than before. This is interesting in relation to the work of Brian & Brian (1951) and Brian (1953) who have shown that the larvae of this species require regurgitated liquid partly, if not solely, to supply their fluid requirements, and that there is a ratio of workers/larvae which is optimally efficient for brood-rearing. Fielde (1901) has recorded that the larvae of another Myrmicine ant, *Stenamma* (*Aphaenogaster*), are fed by regurgitation when young, and with shredded insect when older. A possible explanation would be that in such species nectivorous foraging is the result of low level stimulation, while high level stimulation results in the collection of insect prey. Further work on this problem might give interesting results.

The observations quoted above all refer to relationships between larva and worker. It is also known however that foraging can be elicited, by callows (Schneirla, *loc. cit.*) and by excited, returned foragers (Lubbock, 1882; Eidmann, 1927; Goetsch, 1937). The foraging elicited in this way does not seem to differ from foraging elicited by larvae or from "spontaneous" foraging. There is no available evidence that hungry, mature workers can stimulate other workers to forage; indeed, soliciting for food is largely ignored except by returned foragers or individuals with secondarily filled crops. It is possible however that in an active colony non-foragers which have themselves been aroused by the brood might stimulate other workers to forage. The part played by reproductive forms must also be remembered, for in early stages of colony formation workers may forage and retrieve food for the queen when no brood is present (Wheeler, 1933).

On general grounds it would be expected that foraging for the brood was a part of the major reproductive instinct (Tinbergen, 1951), while selfish foraging was a part of the major feeding instinct. If this separation of different instincts is valid for ants, then in species which have an entirely carnivorous, or a mixed diet, the same behavioural mechanism has been shared by two different instincts. This sharing of a common pattern has been described for birds by Hinde (1953) and Lorenz (1937), who called it "Werkzeugreaktion", but in birds it is usually only a part of a behaviour pattern which is shared.

The Stimuli Releasing Foraging Behaviour

It was suggested in the previous section that an ant may forage "spontaneously," and in response to the presence of larvae, callows, or returned foragers. The nature of the stimuli which release foraging will be discussed below.

The part played by an ant's own viscera in stimulating foraging would be difficult to investigate. It seems legitimate to assume, however, that the viscera do supply such stimuli. In a colony with no brood the activity of the workers is very slight, which might suggest that visceral stimuli are of little importance: however, the general activity of the workers might increase their metabolic rates and indirectly lead to greater visceral stimulation. Except in those ponerines which forage individually for nectar and do not regurgitate (*vide supra*), the foraging of the individual in response to its own hunger may lead to the retrieving of food for other members of the colony, as apparently occurs in *Eciton*.

The stimuli by which the larvae excite the workers to forage are largely tactile. The larvae of *Eciton* (Schneirla, 1938) and of *Myrmecia* (Haskins & Haskins, 1950) have very mobile and muscular heads and thoraces. The writhing of the larvae brings them in contact with workers who receive quite sharp blows from the larval heads. This causes the workers to become "excited" and some at least leave the nest on a foraging expedition. Schneirla showed that freshly killed, and therefore motionless, larvae did not excite workers in this way. This is also true of *Camponotus pennsylvannicus*, where diapausing and motionless larvae do not attract much attention from workers and do not cause foraging (personal observation). Schneirla has suggested that some chemical factor might also be involved here, but this seems unlikely for three reasons:

(*a*) Freshly killed larvae would presumably retain some exudates for a short time, at least, after death, but in fact do not excite the workers.

(*b*) In *Myrmecia* the exudates do not play a very great part in trophallaxis.

(*c*) It is difficult to see how an attractant chemical, which is eagerly licked by the workers could excite them to leave the source from which it comes, unless it were an intoxicant.

In *Eciton* the developing larvae are spread widely through the bivouac, instead of being isolated in a small packet, as are the eggs: this ensures that they have greater opportunity to stimulate more workers, and so increase the supply of food to the nest. Royal larvae are larger and are more efficient at stimulating workers than small larvae.

In the above paragraph the term "excited" was used to describe the workers' behaviour after stimulation from the larvae. It is questionable whether this "excitement" is of a general nature, or whether it is restricted to the foraging behaviour. This will be further discussed later.

The stimuli by which callows and returned foragers excite other workers are of a similar tactile nature to those given by the larvae. The callow or returned forager runs excitedly about the nest and gives sharp blows to other workers with its head, forelegs, and antennae (Goetsch, 1934; Wasmann, 1899; Forel, 1928; Barnes, 1941; Eidmann, 1927). This excites some workers which then may leave the nest in search of food. The difference between these excitatory stimuli and those used for soliciting for food by regurgitation seems to be the more gentle and caressing nature of the latter. It is again possible that the excitement of the workers receiving the sharp tactile stimuli is not restricted to foraging behaviour, for the same sort of stimuli are supplied by workers which may have returned from other colony activities such as digging, fighting, retrieving brood, or moving the nest. The canalising of the behaviour of the excited worker into one of these activities may depend on the subsequent behaviour of the returned forager, or upon other members of the colony (see later).

It will be seen from the above that the stimuli by which both brood and workers arouse prospective foragers are tactile; the recipient is subjected to fairly sharp blows from the head or appendages of the donors. Since such stimuli are rather unspecific, both brood and workers can successfully produce them, and can thus utilise the same behavioural mechanism of the forager: this seems to be an economical situation both in terms of perception and of action.

Feeding Behaviour and its Releasers

When an ant is searching for food it may take either liquid or solid material, and may obtain either of these direct from the source of food, or indirectly from a returned forager. There are therefore four feeding situations to be considered—the collection of insect (or other animal) booty in the field, the collection of nectar in the field, the distribution of booty within the nest, and the activity of regurgitation. These four activities will now be considered.

(a) The Collection of Booty

The type of booty collected by ants is sometimes very specific, as in the Dacetines which take only a few types of Collembola, and sometimes very general, as in the Dorylines which take almost any animal tissue. Where the diet is restricted there is a corresponding stereotypy of hunting behaviour and the stimuli releasing it, while in species with a catholic diet it seems difficult to analyse either specific behaviour patterns or stimuli.

Wilson (1953) and Brown (1953) have shown that epigaeic Dacetines feed only on a few types of Collembola, rejecting other potential prey. The behavioural sequence involved is as follows:

1. The forager stalks slowly and stealthily along with its mandibles held wide apart.
2. When the ant passes within about 1 mm. of a collembolan, which it perceives by its odour, it turns towards its prey and moves very slowly forwards.
3. When the collembolan touches the two sensory labral spines, which project forward from the labrum of the ant to a point where the tips of the mandibles meet, the jaws close with a snap, impaling the prey. Movement may be an important stimulus here, as an ant was sometimes observed to stir a collembolan with its antennae, closing its jaws only after it had moved against the labral spines.
4. If the impaled prey struggles the ant rears up bringing its abdomen forward and making stinging motions. Although stinging often seems to be incomplete the prey soon becomes motionless as a result of the treatment.

The Dacetines thus show a stereotyped hunting behaviour, with each particular activity in the sequence released by a specific stimulus.

The behaviour of more generalised carnivores, such as the *Ecitons*, cannot be analysed so successfully in this way. The Army Ants tend to enter crevices, particularly those which are damp and dark (the response to light being mediated through the ocelli, Werringloer, 1933). This naturally increases the probability of finding prey. It also seems probable that foragers may be attracted by and towards the odour of almost any animal tissue. Once the prey is contacted the foragers swarm over it, biting whenever a movement occurs: an *Eciton* will subsequently open its jaws only after a portion of the prey has been torn off for portage. It seems that the movement of the prey is an important stimulus here, for some long-legged insects have been observed standing motionless and unharmed in a foraging swarm; however, biting will also occur in the absence of movement by the prey. *Ecitons* do not sting their prey, but rely on the effect of a mass of foragers biting and tugging at the same time.

Even in species with more highly developed eyes the visual sense is not important in the discovery of prey, perhaps because at their best the compound eyes of worker ants contain only a few hundred ommatida (Werringloer, 1933), and are ill-suited to the perception of anything but coarse movement. The reaction to a moving object in the vicinity is usually either flight or threat, neither of which lead to the capture of prey. The habit of searching in crevices is obviously adaptive for species not dependant on sight. When potential prey is in the open ants will often pass by unheeding within a few centimetres' range. *Formica rufa* (Chauvin, 1950) and *Lasius niger* (Lubbock, 1882) often pass by close to a struggling fly without perceiving it. When the prey is noticed it is apparently due to its odour. Lubbock has recorded how *L. niger* responds to such odour by turning its antennae towards the source of the odour and walking slowly forward in an exploratory manner, moving its antennae slowly from side to side until finally making contact with the prey. Once contact is established the behaviour of the ant again seems to depend on the prey; if this moves actively the ant may show flight and attack successively, making several advances and retreats (the "dance" of *Dorymyrmex* described by Goetsch, 1937) before finally biting and stinging the prey; if the booty is motionless (e.g. if already dead) the ant may still bite and sting it. When the prey is finally submissive the ant usually examines it carefully, and crawls upon it; Chauvin (1950) suggests that during this period the booty acquires some of the ant's odour, and that the forager will only retrieve booty with such odour.

The forager may carry the whole of the booty back to the nest in its jaws, detach some part of it for portage, or return empty-jawed to the nest to arouse other workers who may then find their way to the temporarily deserted food. Chauvin (1950) and Lutz (1929) have shown that individuals tend to carry loads most suited to their size—the large workers taking the heaviest burdens. The apparent co-operation of several individuals to retrieve a heavy burden is the result of each individual attempting to carry the booty home itself, a process which sometimes, but not always, results in speedier transport than when working in isolation.

If a returning forager is deprived of its load it commences to make searching movements, and does not return to the nest. It seems that the stimulus of food in the jaws may therefore release the behaviour of searching for the nest. However, the fact that an ant will return empty-jawed to arouse other workers shows that other stimuli may have the same result.

(b) The Collection of Nectar

The sources from which ants collect nectar are notable for their great variety, and are both animal and vegetable. Ants will take nectar from both floral and extra-floral nectaries and indeed from any place where a plant exudes sweet sap. The habit of searching in crevices is again advantageous to the forager here, for nectaries are often situated at the bases of flowers and leaves. It is not known whether odour or colour is of use to the ant, but it seems quite possible that an individual forager might learn to associate such stimuli with food, the sensory apparatus being quite adequate: an investigation of this problem might prove interesting.

The association of ants with Aphids has been well known since Huber (1810) recorded it. It is now known that ants will take sugary excreta from a wide variety of Homoptera, and also from Lycaenid larvae (see Forel, 1928). The subject has recently been surveyed by Nixon (1951), and further contributions made by Way (1954 a & b), who have shown that except in a few cases (e.g. *Lasius flavus*, *Oeco-*

phylla longinoda) the relationship between ants and Homoptera is not as close as has been previously supposed. The shelters built by the ants around the "cattle" are to shelter the ants themselves rather than the Aphids, and the pugnacity shown against predators is self-defence from which the Aphids benefit only incidentally. The removal of the excreta also benefits the Homopterans, for too great an accumulation of this has deleterious effects on the population. Nixon suggests that the behaviour of the ant in collecting the honey dew is little different from its behaviour in obtaining nectar from floral sources: it seems possible, however, that the caressing movements which the ant makes with its antennae to persuade the Aphid to yield its excreta slowly, may resemble those used in soliciting for larval secretions in the nest, and may be learned. Ants will attack Aphids or Coccids from which they have previously taken honey dew; the attack is stimulated by any sudden or jerky movements by the Homopterans, and presumably resembles the normal ant responses to prey. The Aphids can defend themselves by a secretion from the cornicles, which is repugnant to ants and other predators. When the relationship between the ants and the Homoptera is not close, it is therefore the behaviour of the latter which governs the response of the forager, which may react to them as either potential prey or as a source of honey dew. When the relationship is close, however, (e.g. the association of *Oecophylla longinoda* and the scale insect *Saissetia zanzibarensis*, Way, 1954 b) the ant plays an active part in storing eggs, and transporting and disseminating the adults and nymphs. Under these conditions, which must involve specialisation of the ant's behavioural mechanisms, the number of species of Homoptera associated with one species of ant become restricted and the symbionts are usually found only together; the disadvantages of this specialisation are balanced by increased chances of survival by the Homoptera and a more certain supply of honey dew for the ant.

(c) The Distribution of Booty in the Nest

A returned forager may distribute its booty either to other workers or to the larvae; recipient workers may also be involved in further secondary distributions. It is not clear whether the distribution of booty to workers involves active participation by the recipients, or whether the forager merely deposits its booty within the confines of the nest. Ponerine queens will bring booty back to an empty nest (Haskins & Haskins 1950), and workers of *Eciton* often deposit their booty in caches along the foraging trail, which suggests that booty may be left in the absence of recipients.

The presentation of booty to the larvae however does seem to occur in response to active stimulation. Tanner and Weber (in Wheeler, 1937) have shown that "pouting" (in and out movements of the mouthparts) of the larvae of Leaf Cutters leads the workers to place balls of fungus in the larval infrabuccal pockets. In *Myrmecia* (Haskins & Haskins, 1950) and *Eciton* (Schneirla, *loc. cit.*) the workers are attracted to moving larvae and place pieces of booty close to or upon them, or alternatively place the larvae on the booty. The queen larvae attract more attention than the male, which suggests that a chemical stimulus may also be important here.

When some ant larvae receive food they secrete a saliva-like fluid which is licked up by the workers (Wheeler, 1918, 1928). It is usually assumed that such secretions are attractant to the workers, and if so they might well function as a "reward" for feeding, which could thus be a conditioned activity. However, Brian & Brian (1952) have shown that in the Wood Wasp, where the behaviour appears similar to that in ants, the larval secretion contains no chemicals attractive to the workers, who promptly regurgitate it outside the nest; the purpose of this process is to eliminate water from the larvae (which have closed anuses) without wetting the fabric of the nest. In view of these observations, the situation in ants would bear reinvestigation.

(d) Regurgitation

A worker may regurgitate the contents of its crop either to other adults or to larvae or to some of the social parasites. A potential donor searches actively for an acceptor, which may be already searching for food, or may be aroused by the donor. The donor arouses acceptors by palpating them with its antennae and forefeet: this stimulus is frequently ignored, but some adults respond by turning toward the donor and returning the antennal contact; both participants then raise their heads, open their mandibles wide, and the donor regurgitates a drop of fluid which is avidly licked up by the acceptor. During the actual food exchange the antennal movements usually change to a slow sweeping type, which is also seen during other

drinking (Heyde, 1924); more vigorous antennal palpation is renewed if the donor moves its position or ceases to yield honey dew (Vowles, 1952). A single acceptor does not usually exhaust the donor, who supplies several acceptors in turn.

Heyde (1924) has studied the development of the feeding response in the callows of various Formicinae. Pupae were removed from the nest and reared in isolation from adult workers, and under these conditions most of the typical patterns of behaviour developed much more slowly than in normal callows. Young callows do not show spontaneous soliciting for food, but develop the oscillatory movements of the antennae and forefeet only after persistent stimulation from adult workers who regurgitate to them; at first the movements of the appendages are simple and unco-ordinated, but after several feedings they develop into the normal pattern. Maier & Schneirla (1935) interpret this as showing that the initial uncoordinated movements of the appendages are due to the "excitement" on being fed, and the later co-ordination of these movements is learned in response to feeding and then used in any potential feeding situation. The activity of regurgitation is similarly learned, the callow requiring persistent stimulation by another worker before it will regurgitate, and being at first unable to control the quantity of fluid which it emits; in this case the stimulus resulting from deflation of the crop might be an additional factor, and may perhaps act as a reinforcement.

Individual Differences in Behaviour

The specialisation of structure involved in the evolution of worker castes has been accompanied by corresponding specialisation in behaviour. In *Camponotus*, for example, the intermediates are most active in foraging and in primary regurgitation, the minors are more concerned with secondary regurgitation, and the majors only with accepting food (Pricer, 1908; Buckingham, 1910; Kiil, 1934; Chen, 1937). This specialisation of behaviour is not totally restrictive, but involves a preponderance of a certain caste in particular activities. This implies that each individual possesses the nervous mechanisms necessary for every activity, but that the threshold of any activity is different in different castes. The same argument can also be applied to the differences in behaviour between the queen and the workers, and it seems possible that the queen secretes a chemical which actively supresses reproductive behaviour in workers, in a manner analogous to the functioning of the "queen substance" in bees (Butler, 1954; Bier, 1954). The suppression of the queen's foraging can be done more simply by the workers in three ways—by keeping her well fed, by removing developing larvae and callows from her vicinity, and themselves clustering around her, and by actively holding her in the nest—all of which seem to occur (see Schneirla, *loc. cit.*).

In addition to these differences between castes there occur differences between individuals of the same caste in di- and trimorphic species and between members of the same colony in monomorphic forms. Thus, hyperactive workers have been recorded by Lubbock, (1882), Fielde (1901), Pricer (1908), Buckingham (1910), Schneirla (1929, 1933, 1942, 1943), Combes (1935), Chen (1937), and Barnes (1941): the phenomenon has also been discovered independently by Morley (1948, 1950 & 1953). It is not known whether these individuals are equally active in different types of behaviour, or for how long their hyperactivity persists. Schneirla, who has shown that the most active foragers are also those individuals who learn to run mazes most efficiently, suggests that less active foragers may tend to remain in the nest and become engaged in nest activities. Although these active individuals are undoubtedly important in initiating group behaviour, until some careful, precise and preferably quantitative observations have been made on the subject it would be unwise to indulge in speculations such as those of Morley (*loc. cit.*).

The Journey to and from the Nest

When an ant leaves the nest in search of food it is faced with two problems of orientation, for it has to guide itself efficiently not only to the feeding place but also on its return journey. The types of stimuli by which the forager orientates itself have been the subject of much study, and only a brief review will be given here.

(a) Visual Stimuli

An ant may orientate by either celestial or terrestrial visual stimuli, which differ in important ways, to be discussed below. The celestial stimuli used are light coming directly from the sun, and the polarised light of the blue sky, produced by diffraction in the upper atmosphere. Santschi (1911, 1923) and Brun (1914) showed that an ant could maintain a particular heading by walking at a constant angle across the sun's

rays—a type of behaviour called the "light compass reaction," which is now known to be shown by many insects. The physiology of the light compass reaction has been worked out in beetles by von Buddenbrock (1935) and in ants by Vowles (1954 b), who have shown that under laboratory conditions the insect may select any one ommatidium as a fixation point and will walk straight ahead when this ommatidium is illuminated, turning back to its course when other ommatidia in the same horizontal plane are stimulated. As Vowles (1954 a & b) has pointed out, however, this analysis cannot be directly applied to behaviour under natural conditions, where the visual field contains many sources of stimulation whose effect must be inhibited, and where the ant may deviate from the true direction in more than one plane. It has also been seen that an ant often maintains a general heading with a fairly convoluted path, rather than the precise and straight track seen in the laboratory.

It is known that ants will orientate themselves by means of plane polarised light (Vowles, 1950; Carthy, 1951). These authors used light only directly above (dorsal to) their ants, and no investigation of the type made by von Frisch (e.g. 1949) with honey bees has been attempted. Under the conditions used the ants maintain a particular heading by making a constant angle across the plane of polarisation of the light from above. Vowles (1954 b) suggests that the analysis of the polarised light is carried out by the only two dorsal looking ommatidia in *M. rubra*, but in view of the results of Waterman (1953) it is possible that the analysis is carried out by ommatidia aligned in directions other than that of the incident light.

Both the position of the sun and its corresponding pattern of polarised light from the sky change with the time of day: this change occurs in both the horizontal and the vertical plane. If an ant is occupied in foraging long enough for the sun to move through a perceptible angle (less than 10 degrees in *M. rubra*, taking about 40 minutes) the ant must be able to adapt for the change, if it is to return home without error. Imprisonment experiments of the type described by Brun (1914) suggest that the adaptation can only occur if the ant is in continual sight of the sun. Some preliminary experiments by Schneirla (1933 *a*), who allowed ants to forage in an arena around which moved an electric light, suggest that the speed of rotation of the light source is important, ants becoming disorientated if this is too high. Apart from these two observations however the mechanism by which ants allow for movements of the sun is not understood.

Lubbock (1882), Brun (1914), and Santschi (1923), among others, have shown that ants may orientate by means of terrestrial landmarks such as trees, or stooks of corn. The observations made, reveal, however, only that ants become disorientated when the landmarks are obscured. It is not known whether the landmarks are used in a temporal or spatial pattern, or individually in isolation. Vowles (1951) showed that if *M. rubra* is allowed to forage in an arena and is exposed simultaneously to a strip of black paper at the side of the arena and a dorsal beam of plane polarised light, the ants home more accurately and rapidly than when exposed to either stimulus by itself, which suggests that the whole visual field may be important in orientation.

When an ant orientates by a terrestrial landmark which is not sufficiently distant to be effectively at infinity, the angle between the ant's track and the direction of the landmark is continually changing (unless the ant moves directly toward or away from the landmark); this may be contrasted to the light compass reaction and to orientation to polarised light where the ant's track makes a constant angle with the direction of the stimulus. Thus the orientation by landmarks must involve different mechanisms from those used in orientation by celestial stimuli (Vowles 1954 a).

(b) Chemical Stimuli

Although ants may be disturbed and possibly disorientated by the presence of a strange odour (Turner, 1907; and Carthy, 1951), it seems unlikely that they utilise the natural odours of the environment as orientatory stimuli. It is well known, however, that ants do deposit an odorous substance to mark their track (Bethe, 1898; Brun, 1914; Santschi, 1923 & 1930; Schneirla, 1944; MacGregor, 1948; Carthy, 1950, 1951) and by depositing a series of such odour spots are able to "blaze" a trail. The odorous substance is an anal secretion (Carthy, 1951) the nature of which is not clear—it may be largely a faecal deposit. The ant makes an odour smear by flexing its abdomen slightly until its tip is on the ground, secreting a drop of the odorous fluid, and dragging the tip of the abdomen along for a few millimetres (Santschi, 1923, 1930; Goetsch, 1937), thus producing

the pear-shaped smear observed by Carthy. The smears are usually deposited when the ant is excited, and are therefore made most frequently on the homeward journey, after the successful discovery of food; however, outward bound foragers will also make smears, and this turns a communal odour trail into an intricate tangle of such smears, with their broad ends pointing both toward and away from the nest. Carthy has pointed out that such odour trails are not polarised, and that a forager striking the trail is not able to identify the nest direction (see also Chauvin, 1948). There does seem to be some polarisation in the *Eciton* odour trails, however, and Schneirla believes that this may be due to the greater concentration of odour toward the bivouac, due to greater incidence of traffic near the nest. MacGregor (1948) has shown that a single odour spot apparently has directional properties in *M. rubra*, and this may perhaps be due to the shape of the smear.

(c) Tactile, Kinaesthetic, and Other Stimuli

Although changing the texture of a surface on which an ant is running may cause some disturbance (Turner, 1907), this is far less than that occasioned by changing the light direction or destroying an odour trail. Tactile stimuli from the environment do, however, play an important part in canalising the ant's tracks. Schneirla has recorded how Army Ants will tend to follow smooth tree roots, and trails worn by peccaries and armadilloes: *Cryptocerus* (personal observation) travels many scores of metres on the lianas without descending to the ground. This type of behaviour, which is the result of taking the path which offers least resistance to travel, obviously allows great rapidity of movement. In some cases, such as the trails of the Harvesting Ants, the passage of many insects itself produces a smooth pathway. Under conditions where such systems of smooth trails are used the situation comes to resemble that of a fairly simple maze, with choice points and blind alleys, such as some investigators have used in the laboratory.

Piéron (1904) suggested that foragers used a kinaesthetic sense when homing, remembering the muscular effort involved in the various turns and twists of the trail. This hypothesis has now largely been discarded (see MacGregor, 1948, and Carthy, 1951), for returning foragers do not retrace their outward path in any except a very general sense. However, many of the laboratory experiments on ant orientation have been concerned only with short distances (a few centimetres), and it seems possible that over longer distances, when an ant has learned a particular route, it may have some potentially useful knowledge of the length of its path, as have bees (Wolf, 1927).

Another stimulus which may be important for orientation is that provided by gravity. Ants will perform a force compass reaction to gravity in the same way as they perform a light compass reaction to the sun (Vowles, 1954 a & b). Turner (1907) and Cornetz (1914) have shown that a forager may be disorientated if the slope of the surface on which it is travelling is changed. Little is known, however, of this aspect of behaviour, and some learning experiments using a vertical maze might yield interesting results.

It will be seen from the above account that an ant has many potential stimuli available for its use in orientation. The extent and way in which they are used will be discussed below.

The track of an ant foraging in unknown territory, or in known territory for an unknown source of food, has a typically convoluted appearance. This searching behaviour is not, however, entirely random; Weyrauch (1935) has shown that *M. rubra* tends to forage in a symmetrical course, and species differences exist —*M. rubra* tends to intersperse its looping track with short straight runs (MacGregor, 1948) while *Lasius niger* walks on a more continuously convoluted course. Species such as the *Ecitons* and epigaeic Dacetines, which depend almost entirely on chemical and tactile stimuli, show a very different type of searching behaviour, which will be discussed later; but even here species differences are found: *E. hamatum*, for example, forages in large swarms, while in *E. burchelli* the "swarm" is split into a series of separate narrow columns (Schneirla, 1940). Too little attention thas perhaps been paid to the differences in behaviour shown by different species.

The convoluted foraging track described above is adaptive, in that the forager covers a broader strip of ground than it would by following a fairly direct course from one point to another, while at the same time not straying far from the nest. Once food has been found, however, the problem of homing and of subsequent journeys becomes one of eliminating the tortuosities of the tracks and progressively straightening the route between the nest and

the food source. In the early stages of this process visual stimuli are important, and the ant travels in a series of fairly straight runs roughly paralleling the general directions of the various branches of the original outward path; looping recurs when the ant is disorientated. During this process odour spots are distributed and the ant runs from spot to spot, orientating between them by vision. As progressively more odour spots are deposited, so the odour trail becomes more marked, and the dependence on chemical stimuli becomes greater. When the odour trail is established the behaviour of the ants changes: the individual now runs rapidly along the path palpating it with one or both antennae, whereas before the trail was established the antennae were held well off the ground while the individual ran between odour spots. It will thus be seen that the relative importance of visual and chemical stimuli changes with the number of journeys which ants have made over the foraging route; this explains the apparent discrepancies between the results of Vowles (1950, 1951), who showed that individuals of *M. rubra* foraging in unfamiliar territory were dependent on visual orientation, and MacGregor (1948), who claimed that large numbers of workers of the same species foraging in familiar environment were dependent on chemical orientation.

The extent to which visual and chemical stimuli are used differs in different species. Various species of *Formica* (Shepard, 1911; Schneirla, 1929) are largely dependent on visual stimuli, and will learn to run complex mazes, orientating the successive branches of their path to the direction of incident light. When an individual has run the maze several times odorous substances tend to accumulate at various points in the maze, particularly at choice points, and disturbance of these does disorientate the ant to some extent. However, the odour is not a special secretion, but results from accidental contact of the ant with the floor and walls; moreover, each individual responds only to its own deposits, and ignores those of others. When ants such as these form a path under natural conditions it is usually fairly broad and is made up of individual rather than common trails.

Species such as *L. niger* (Carthy, 1951) and *M. rubra* (*vide supra*) depend more on odour than do *Formica* species. As suggested above, the odour spots are a definite anal secretion, but the trail becomes established only after a considerable number of foraging trips has been made. With ants such as *Lasius fuliginosus* (Carthy, 1951), and *Tapinoma*, *Pheidole*, and *Solenopsis* (Santschi, 1930; Goetsch, 1937) the trail becomes established much earlier and, indeed, a single forager may mark out a fairly adequate route on a single journey by depositing a series of odour smears. In such species, which establish definite odour trails, the chemical is specific to the colony, and not to the individual (observations have also been made of ants following the trail from another colony, but this is infrequent), and the path is narrow compared with that used by *Formica*.

The use of chemical and tactile stimuli has been carried to its extreme in the Dorylinae. Schneirla (1938, 1940) has shown how the Army Ants when leaving the bivouac lay down a concentrated chemical trail as they progress along their outward route: workers forced from the bivouac by the "pressure" of aroused nestmates, congregate in the parts of the swarm where booty is found, and the odorous secretions accumulate here; this odour attracts more workers, thus concentrating the outward "pressure" at these points and "ballooning" the swarm out again, after which the process is repeated. Behind the advancing swarm the trail thus becomes canalised by the concentrations of odour; more ants then pass over the route, depositing more odour and establishing the trail even more markedly. Schneirla analyses the whole complex pattern of the Army Ant's raiding system into a few simple factors—pressure from within the bivouac (caused by a turning away from strong tactile stimuli, and towards weak stimuli), which becomes canalised along the trail to the raiding front, thus forcing the swarm on; the concentration of ants where booty is found; the tendency to travel on smooth surfaces such as exposed tree roots; and the tendency to run rapidly over surfaces impregnated with trail odour, but to move forwards only hesitantly, continually turning back, when on a fresh surface. Vowles (personal observation) found that workers on a fresh surface sometimes tended to turn alternately to either side; if one antenna was amputated the ants would only turn towards the intact side on a fresh surface, but would run straight on one impregnated with trail odour; callows which had been isolated and artificially removed from the cocoon did not follow a colony trail, and showed the side to side turning movements both on fresh surfaces and those impregnated with

colony odour; amputation of an antenna again caused unilateral turning, on both surfaces. A possible interpretation of this is that the side to side movements are innate, and that the ants learn not to turn away from the side stimulated by trail odour—a process which will tend to bring them back to the trail once they have left it, although it will not suffice to produce running along the trail once regained. For more adequate details of the theory of trail-following in *Eciton*, the reader is referred to Schneirla's papers (*loc. cit.*).

The Influence of General Environmental Stimuli

In addition to the function of stimuli in releasing particular behaviour, and in orientation, the environment also supplies stimuli which exert a general effect upon the activities of ants. The three factors which are most important are light, temperature and humidity. The activity of many species shows a fairly marked diurnal rhythm, commencing in the early morning and ceasing at night, although many desert icolous forms are active during the night, particularly in the moonlight (Santschi, 1923).

Schneirla (1938) has shown that the foraging of hypogaeic *Ecitons* starts with the first increase of dawn light, before the temperature has risen; foraging activity then increases through the morning, decreases at midday, builds up again during the afternoon and decreases again as the light fades. Epigaeic species, on the contrary, do not show such a marked rhythm. A similar pattern of activity has been shown for temperate zone species by Talbot (1940, 1943) and Kennedy and Talbot (1940), and for species living in hot, dry climates by Buxton (1924) and Pickles (1946). The midday lull in activity is most marked in desert-icolous forms, and in the dry season in the *Eciton's*: its adaptiveness lies in reducing water loss, which would be greatest at midday, when humidity is lowest and the temperature highest. It is not clear whether the reduction in activity is due to the actual change in humidity, or to overstimulation by light and heat (which does induce torpor), but probably all three factors are involved. The cessation of activity is not merely a negative process however, for the ants actively seek dark, damp and cool places in which to rest, which suggests that specific taxes or kineses are involved. The actual increase in activity due to light and temperature (Talbot, 1943; Shapley, 1920; Pratt, 1925; Abbot, 1927; Barnes & Kohn, 1932) seems to arise in different ways; the effect of a rise in temperature is presumably to increase the general metabolic activity of the ant; light, however, must act through the visual receptors, presumably to raise the level of nervous activity in the central nervous system. It is interesting in this context that Hoagland (1931) showed an increase in the rapidity of learning when the temperature was raised, although such an effect would not be expected with brighter illumination.

General Discussion

Perhaps the most significant point which emerges from any survey of ant behaviour is the extreme diversity of the habits of different species. Indeed, the Formicidae present an ideal group for comparative studies of behaviour, for even foraging activities show great variation, ranging from the extreme stereotypy of Dacetines and Attinines to the general adaptability of the Formicines. The ability to make use of a wide variety of food is obviously an advantage when there is a limit to the food available within the foraging territory. The fact that the Dorylines, with their carnivorous diet, are largely restricted to tropical areas suggests that under temperate conditions, where insect numbers are smaller, even such a general diet would rapidly exhaust the available food supply; the restrictions of the temperate conditions seem to have necessitated the development of the partially nectivorous diet. Even under tropical conditions, however, there are few species with fixed nests which have large colonies. The nomadic behaviour of the Dorylines which have large colonies seems to have evolved as a precaution against the possible denudation of the territory, although as Schneirla has shown, the migrations are not directly related to the availability or lack of food. It is significant that species with specialised foraging habits have all exploited a type of food which is abundant and not competed for by other ants: the Dacetines, for example, collect Collembola, which are too small and active to be caught by ordinary biting and stinging, and the Attinines collect green leaves to act as substrate for the fungi on which they feed.

Although the adaptiveness of the different types of foraging behaviour is fairly clear, and throws some light on the evolutionary history of these habits, the development of the behaviour within any individual raises further problems. In a group which exhibits such marked learning

ability it would be surprising if some of the sign stimuli and their corresponding activities were not learned. Where the diet is varied and an individual collects different sorts of booty, which require different methods of handling and give out different stimuli, it would be expected that the innate component of behaviour would not play a dominant part. The effect of larval diet upon adult foraging behaviour would be an interesting field of study, for it is conceivable that some form of preimaginal conditioning (Thorpe & Jones, 1937) may play a part in determining food preferences in the adult.

It is clear from the work of Heyde (*loc. cit.*) that both soliciting for and regurgitation of nectar involve a strong element of learning. The stimuli and the activities involved here are very simple, and do not require any complex nervous mechanisms for their control. The stimuli releasing foraging behaviour are similarly very simple—tactile stimuli from contact with moving larvae, callows or returned foragers. The very simplicity of these stimuli introduces a complication, however, for if the stimuli are simple they are also unspecific. There are many activities which are causally related to stimuli from members of a colony, and yet the stimuli which an ant or its larva may give are potentially very limited—visual patterns must be almost eliminated (by the epigaeic nesting habit), there seems no particular code in antennal vibrations, and the number of glandular secretions made available externally is small. It is therefore difficult for an ant to provide different stimuli to release different activities. This difficulty has been overcome in two ways:

1. By utilising the state of the reactor and the environmental situation. Thus, when an ant with a full crop has its regurgitatory behaviour released, the stimulus situation to which it reacts is composed not only of the tactile stimuli from the antennae of the solicitor, but also of the stimulus arising from the inflation of the crop. Similarly, when a forager deposits booty upon larvae it receives stimuli not only from the larvae and the nest, but also from the booty which it holds.

2. By utilising the statistical properties of populations. In the discussion of the stimuli which release foraging it was suggested these were of a simple tactile nature, and being fairly unspecific could be given by larvae, callows and adults equally well. It was further suggested that the effect of these stimuli was to cause a worker to become "excited," this term being descriptive of the agitated behaviour of the worker. Schneirla has suggested that this excitement (or excitation?) is not specific to the foraging "drive," and the evidence available does not allow us to decide this issue. It remains possible therefore that the stimuli which are supposed to release foraging do in fact have a general excitatory effect, lowering the threshold for many activities (bringing the worker into the "mood" for such activities), the subsequent behaviour of the worker being determined by the stimuli it later encounters—thus, if finding an odour trail the ant may follow it to food, if coming to a situation in which building is required it may build. If the situation is of this nature it may well be that the ant's behaviour is organised on a hierarchical basis (see Tinbergen, 1951), and that the tactile stimuli act at a high level in this hierarchy. If this is so, the system has the disadvantage that hungry larvae, callows, or returned foragers could not necessarily stimulate other workers to forage. This problem is not grave, however, if the population is fairly large and if more workers are stimulated than are necessary for foraging, since there will always be a high probability that some at least of these workers will come into a feeding situation.

When larvae or callows supply the stimulus there can be no question of their directing the excited worker to any particular food source: however, such an ant may remember previous feeding places and return to them (as Schneirla has shown for *Formica*), or may follow an established odour trail. When a returned forager arouses other workers it is possible that they may, however, be directed to the food-source: this may be done in two ways, firstly by the secondarily aroused workers following the original forager when it leaves the nest again (a type of behaviour which can be easily observed), and secondly by following an odour trail left by the returned forager. Goetsch (1934) has suggested that an excited forager may stimulate other workers by glandular excretions as well as by antennal contacts; if the returned forager produced some of its anal secretions, the aroused workers might well search for this odour in the field and so be led to the food: this is a piece of behaviour comparable with that of honey bees when one forager marks flowers with its scent for others to find.

A tentative scheme classifying the different aspects of foraging behaviour may now be

proposed. The various events which occur are as follows:

1. A prospective forager is excited by tactile stimuli from larvae, callows or returned foragers. As a result of this the ant runs about in an agitated manner until reaching a stimulus situation in which its behaviour becomes canalised into a particular activity. The part played by the ant's own viscera in contributing to the excited state has not been evaluated.

2. If the excited forager encounters another ant it may follow it into the field and thus be led to a food source. If a returned forager has laid a fresh odour trail the new forager may follow this trail to the food. If the new forager has learned to forage in a particular place it may go to that place again. Or the new forager may wander in a "random" manner until it finds some food.

3. When food is perceived it is collected. The stimuli involved and the actual behaviour of the ant depends largely on the species, and both characters are very variable.

4. When the ant has food in its jaws, or its crop is inflated, it starts to search for its nest, utilising previous experience of the environment to return home economically.

5. When reaching the nest the returned forager searches for individuals to receive the food. The "pouting" movements of the larvae stimulate the forager to feed them. Regurgitation is elicited by palpation with the antennae and fore-feet.

Although this scheme is undoubtedly oversimplified, it is hoped that the complications have been indicated sufficiently clearly in the general text to dispense with repetition. The value of such a scheme lies not in its explanatory value, which is low, but in clarifying the problems involved. Only by precise formulation of these problems can the full value of future work in this field be realised.

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TRANSFERENCE OF "IMPRINTING" IN A WILD GOSLING

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Imprinting, as defined by Thorpe (1951), is a very stable form of learning by which the young of social species come to recognise certain supra-individual characteristics of their own kind. It is rapid, does not appear to require immediate re-inforcement and is believed to be confined to a short period of early life. Although originally thought by Lorenz (1935) to be totally irreversible, it is now generally agreed that this is not invariably so. It is still, however, the least studied and least understood form of learning. The following case in which the taming of a wild gosling included a type of learning which had the appearance of a re-imprinting with respect to man, is felt to be of interest for the evidence it shows of a relation between imprinting and the process of habituation.

The object of this study is a lesser white fronted goose, *Anser erythropus* (L.), which was captured in July, 1953, on the breeding ground in North Norway when between one and two weeks old. It was one of a small flock of six adults and ten goslings which were observed on several occasions in the vicinity during the previous four days. On the day of capture it had become separated from the parent flock, which was never seen again. Later the same day it was brought into a camp occupied by the author and three other persons, where it remained under observation until brought back to Britain about five weeks later. It is now in the collection of the Royal Zoological Society of Scotland.

The significant events took place during its first week in captivity, and a brief description of the environment to which it was subjected during that time is therefore necessary.

The camp was situated in meadowland and centred upon an unoccupied farmhouse which was used as a field laboratory. A cage was improvised out of a Government sparrow trap, which was placed on the grass close to the house, and moved to a fresh position each day. The rear of the trap was covered over and fresh grass and water provided as often as required. During the first few days the bird was released to graze at frequent intervals under supervision, but was not handled or driven except for the minimum required to make it return to its cage after feeding. At first it fed almost exclusively on the flower heads of *Poa annua*, which were plentiful around the house, but later developed more catholic tastes in vegetation.

The significant observations on its behaviour during the first few days in captivity are best summarised from the field notes as follows:

1st Day.

Captured during the afternoon and brought to camp late the same evening. Attempted continuously to escape and to avoid recapture. Hissed when approached and uttered alarm call continuously in the presence of human beings. Defaecated repeatedly when handled. When grasped firmly however it ceased to struggle after a time and lay quietly.

2nd Day.

Retreated from contact with human beings, retiring to the inner covered part of its cage when approached, and hissed. Would come out to feed when the door of the cage was opened only if the observer retired a few yards and remained still. After feeding could be gently driven back into the cage by approaching slowly with outstretched hands, when it would retreat rapidly uttering alarm call.

3rd Day.

Behaviour much as on previous day, but a little bolder and tending to wander further from the cage when grazing. More difficult to drive back into its cage, having learned to bypass the entrance and run around to the rear. No longer hissed at close approach of observer.

4th Day.

Handling and close contact with human beings still avoided, but now drawing attention to itself by running to the cage door and calling at sight of the author or colleagues. In this way it demanded more frequent spells of grazing.

5th Day.

Came to author's call of "gek, gek" from a distance of about twenty yards and began to feed in his immediate vicinity. This performance was repeated twice when the observer withdrew a similar distance. Also permitted a little handling, though nervous and tended to run away at any sudden movement or loud noise.

6th Day.

Change noted in behaviour towards author this morning. When released from the cage it came running to "gek, gek" call and followed closely. It was immediately taken for a walk to a point about 300 yards distant from "home," about ten times the greatest distance previously ventured. It followed within a yard or two and whenever author stopped it came right up and touched his foot with its bill. Distinguished between known and unknown territory; wandered freely within a distance of about forty yards of home, taking little

notice of anyone present, but when further away remained close to author. Attempted to follow into the house but fell trying to leap the doorstep and did not attempt this again until two days later.

Allowed itself to be handled freely, but nervous and defaecated repeatedly when lifted from the ground. Later in the day it would follow any of the four members of the party.

From this time it was allowed complete freedom around the camp during the day, being shut in its cage only at night or when all persons were absent from camp.

7th Day.

Now follows all members of the party, showing signs of distress when left alone. Discovered river nearby and spent several minutes in the water. Would not leave until satisfied but then came to "gek, gek" call. From this time on it would frequently call and lead observer towards the water.

8th Day.

Now enters house of its own accord, usually sitting to roost close to the front door, but sometimes close to or in contact with an observer's foot. If the foot was moved it would half rise and shuffle close to it once more.

There is no point in following the day to day sequence of events further, but the following additional observations are worth recording:

1. From the 7th day the goose would follow and allow itself to be handled by the author or by any of his colleagues, but not by visitors to the camp.

2. After grazing it frequently entered the house to rest and preen, often selecting a position close to a human foot and therefore frequently under the table. During the next few days it showed progressively less alarm at sudden movement or loud noises and became eventually completely accustomed to the normal activity and converse of human beings at close quarters in a confined space.

3. Hissing at human beings was not observed after the second day in captivity, but it continued to hiss at horses, goats and dogs.

4. Since it has been at the Zoological Gardens in Edinburgh it has continued to show attachment to human beings but has shown little interest in a pair of black swans, with which it now shares a paddock.

Comments

The interest in this case lies in the relation between the habituation of the goose and its re-imprinting, or perhaps, more accurately, the transference of imprinting from its own species to man. The process of habituation, observed as the decline and eventual disappearance of alarm and flight tendencies, such as hissing, uttering the alarm call, defaecating, etc., in the presence of human beings, was continuous until all normal human activities were tolerated at close quarters. This type of learning is familiar in the process of taming any wild animal, and as Hediger (1950) pointed out is the minimum necessary for making life in captivity tolerable for it.

By contrast the imprinting with respect to man appeared as a revolution in the bird's behaviour on the sixth day in captivity, when the author and his colleagues became objects to be followed. The process was perhaps not so sudden as its more dramatic symptoms seem to suggest. Certain events were noted during the previous two days which have a bearing on the subsequent imprinting and could be regarded as symptoms of its initial stages. Thus, already on the fourth day the bird was calling to be released from its cage when it saw a human being, although once free it kept a definite flight distance between itself and the man, and if the latter attempted to approach more closely it retreated uttering the alarm call. The following day it showed more positive signs of attachment to man in coming towards a call of "gek, gek" and feeding within a yard or so of the observer.

One cannot of course establish causal connections from case observations of this kind, but the sequence of events suggests that the transference of imprinting may be causally related to the habituation process in some way. Social animals are normally attracted to others of their own kind, and imprinting during a definite period of early life seems to be the mechanism by which this attachment is effected in geese and many other birds. In this case we may assume that, although removed by capture from its normal society, the young bird's need of an object towards which its social behaviour could be directed was not affected, and in due course its imprinting was transferred to man. This could only take place however after the wild bird's natural tendency to flee from man was much diminished, until as it were a criticial threshold in the habituation process was passed which permitted the subsequent switch in its behaviour.

It seems likely that the relation was to some extent reciprocal, the transference of imprinting to man in turn facilitating the final stages of habituation, leading to its complete integration within the human social unit.

One is all too aware of the provisional and

incomplete nature of this interpretation. Other types of learning have been disregarded, and it has been assumed that we have not been dealing with an abnormal individual, whose initial imprinting to its own species was defective in some way.

I wish to acknowledge the interest and co-operation in this study of my colleagues on the Edinburgh University Expedition to Arctic Norway, 1953.

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THE MATURATION OF BEHAVIOUR IN HYPOTHYROIDISM AND STARVATION

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Thyroid deficiency in man invariably leads to severe mental dysfunction, and the results of replacement therapy appear to be related to the age at which the disease first appears. In myxoedema, for instance, where the central nervous system has matured before the onset of the disorder, the ensuing mental deterioration responds well and consistently to treatment with thyroid hormone. In congenital hypothyroidism, on the other hand, the results of such treatment are very variable. Cases have been reported in which cretins treated with thyroxin have achieved I.Q.'s well above the average, but on the whole the most that can be expected is an I.Q. of 70 to 80.

The several views which have been put forward to account for this variability (see Topper, 1951) can be divided into two main groups. The first, and most widely held, lays emphasis on the age at which treatment is begun and the adequacy with which it is pursued, implying that the absence of thyroid hormone during early development causes irreversible damage to central nervous tissues. On the other hand, some investigators have been unable to establish any positive correlation between the age at which treatment was started and its ultimate success and have suggested that, where therapy is unsuccessful, this is due to the co-existence of some other congenital abnormality such as might be caused by a genetic factor which governs the development of both nervous system and thyroid gland, or by a "catastrophe" during gestation at some critical stage of the development of both organs. Little experimental work has so far been done, however, to elucidate this problem.

Infant rats can readily be made hypothyroid, and since their brains are very immature at birth the effects of uncomplicated thyroid deficiency on the maturation of the central nervous system can be studied by comparing their behaviour with that of normal littermates. In the experiments reported in this paper, this method has been used to study the development of both innately organised and adaptive behaviour in normal, starved, and hypothyroid rats, and the degree of recovery which follows subsequent replacement therapy.

Materials and Methods

Young albino rats from twenty litters were used for these experiments. About half the rats from each litter were made hypothyroid either (*a*) by giving, on the day of birth, a single intraperitoneal injection of 100 μc radio-active iodine (^{131}I) in the form of an aqueous solution of sodium iodide (Goldberg & Chaikoff, 1949), or (*b*) by giving daily injections of the thyroid depressant drug methyl thiouracil in the doses stated by Eayrs (1954). The remaining rats in each litter acted as controls and were injected with equivalent amounts of the appropriate vehicle. These controls were divided into two equal groups, one being allowed to suckle normally while the feeding of the other group ("starved" rats) was restricted in such a way that their weight at 24 days old was equal to that of their hypothyroid littermates.

When 25 days old these rats were regrouped and treated as under:

Group 1—*Control rats.* Given daily subcutaneous injections of normal saline equal in amount to that given to the rats of Group 4.

Group 2—*Starved re-fed rats.* Starved rats, now given access to unlimited food, and also given control injections of normal saline.

Group 3—*Hypothyroid rats.* Consisting of (i) methyl thiouracil-treated rats now given the drug mixed with the food, and (ii) radio-thyroidectomised rats; all given control doses of normal saline.

Group 4—*Medicated hypothyroid rats.* Consisting of (i) methyl thiouracil-treated rats whose treatment was now discontinued, and (ii) radio-thyroidectomised rats injected daily for 50 days with 2 μg l-thyroxin sodium (Glaxo) dissolved in 0.1 ml. normal saline, and for the rest of the experiment with 3 μg per day.

The rats were put through the tests of behaviour noted in Table I. The way in which the tests were carried out is, for convenience, described with the results.

At the end of the tests the animals were killed and the tracheal region of all rats which had been treated with radio-active iodine was

examined histologically in serial-sections to ensure that no appreciable amount of functioning thyroid tissue was present.

Results

Sensitivity to Cutaneous Stimulation

Each rat was put into a small box which limited its movements, and saline-pad electrodes were applied to its feet. Successive condenser discharges at equally spaced intervals of voltage were applied to the electrode and the intensity of the stimulus required to evoke the first reflex response of the thigh muscles was recorded.

The maximum stimulus necessary to elicit a response did not change significantly between the 4th and 18th day of age in the normal and hypothyroid animals. That for the starved rats was, however, elevated during the first few days of testing but subsequently fell to a level below that of the normal. This decrement in the sensitivity threshold was statistically significant (Table II*a*).

Reflex Suspension

The fore-paws of each rat were touched against a horizontal wire, and the length of time the rat grasped the wire before releasing its grip and falling was measured. The results (Table II*b*) showed that the duration of clinging increased progressively as the rats grew older. There was no difference between normal and starved animals in the rate of increase, but the mean clinging-time of the hypothyroid rats increased more slowly than that of the rats of the other two groups. In addition, whereas from about 10 days old, both normal and starved animals made movements characteristic of climbing (treading with the hind limbs and attempts to flex the fore-limbs), this form of activity was much less marked in the hypothyroid rats, which tended to hang passively.

Duration of After-discharge

Each rat was placed in a small calico bag hung from the arm of a lever so arranged that an electric circuit was made and broken in response to vigorous movements. The interruption of the circuit was used to activate a marker writing on a smoked kymograph drum. When the rat had settled down, its tail was pinched with a pair of forceps made of watch-spring (giving a stimulus of constant intensity.

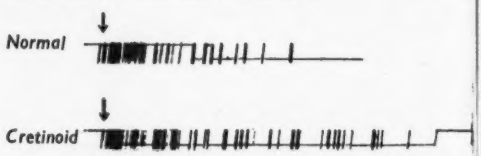


Fig. 1. Kymograph trace showing characteristic pattern of activity in 7-day old rats after compression of the tail (see text).

A typical record of the pattern of activity which follows such a stimulus (Fig. 1) shows that the reflex twitch which accompanies the stimulus is followed by a short pause, after which the rat is thrown into violent and often

TABLE I. Tests of Behaviour Applied to Normal, Starved and Hypothyroid Rats

Age of rat	Test	Class of rat tested
5—15 days	Peripheral sensitivity to electrical stimulation	All rats
5—15 days	Reflex suspension	
5—12 days	Persistence of after-discharge	Radio-thyroidectomised, starved and controls
9—24 days	Startle response	Methyl thiouracil treated, starved and controls
12—24 days	Body-righting reflex	
12—24 days	Placing reflex	
30—50 days	Motor co-ordination test	
60 days to end of experiment	Elevated spatial T-maze	Radio thyroidectomised (treated and untreated), starved and controls
60 days to end of experiment	3-table test	Methyl thiouracil-treated, (subsequently discontinued), starved, and controls

convulsive bodily activity. Periods of such activity alternate with intervals of immobility which gradually increase in length. The duration of this activity was measured on the kymograph record from the reflex twitch until the beginning of the first quiescent interval, lasting 10 secs.

Fig. 2 shows that the activity decreases in amount as the animal grows older and disappears in the normal starved rat at about the 10th day of age. Its disappearance was delayed until the 12th day in the hypothyroid rat in which the mean duration of the activity was significantly greater than that of either the normal or starved animals (Table II*c*).

Startle Response

With the rat held upright, a sharp click was made behind its head and the age recorded at which the first motor response (a jerk of the head and hind limbs) occurred to the auditory stimulus. The results, as determined by the probit analysis of the mean age at which 50 per cent. of the rats responded to the stimulus, show that the response appeared significantly later in both starved and hypothyroid rats

TABLE II. Effect of Hypothyroidism and Starvation on the Maturation of Automatic Behaviour

Response	Unit of measurement	Class of rat			Difference from control ± Standard error (S.E.)	Significance of mean difference
		Control	Starved	Hypothyroid		
(*a*) Change in sensitivity to cutaneous stimulation	Arbitrary unit directly related to voltage applied — units per day	−0·54	−2·60	+0·09	*Starved* −2·06±0·677	P<0·01
					Hypothyroid 0·63±0·397	P>0·3
(*b*) Change in duration of suspension	Seconds per day	0·89	1·12	0·43	*Starved* −0·23±0·259	P>0·5
					Hypothyroid 0·46±0·160	P<0·01
(*c*) Mean duration of after-discharge	Seconds	13·9	15·3	22·6	*Starved* 1·6±3·04	P>0·5
					Hypothyroid 11·7±3·79	P=0·02–0·01
(*d*) Startle response	Age at which 50% of rats give positive response	10·8	12·1	16·1	*Starved* 1·3 (0·050±0·0172)*	P<0·01
					Hypothyroid 5·3 (0·175±0·0161)*	P<0·01
(*e*) Righting reaction	ditto	16·1	19·1	24·5	*Starved* 3·0 (0·076±0·0148)*	P<0·01
					Hypothyroid 8·4 (0·183±0·0143)*	P<0·01
(*f*) Placing reflex	ditto	16·5	17·8	23·5	*Starved* 1·3 (0·033±0·128)*	P=0·02–0·01
					Hypothyroid 7·0 (0·052±0·112)*	P<0·01

* Difference between LD50±S.E.

than in the normal but that the hypothyroid animals were more severely affected than the starved (Table II*d*).

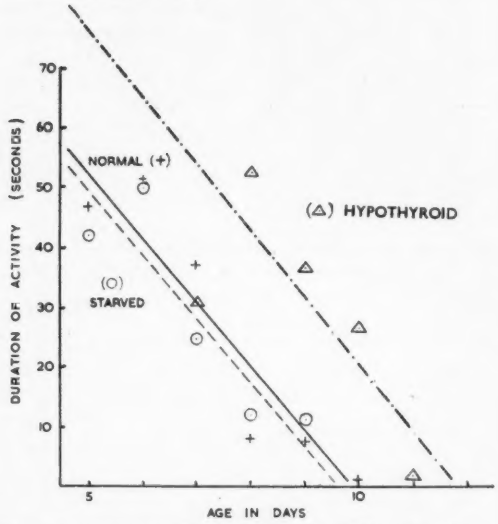


Fig. 2. Increase in the duration of activity following compression of the tail (seconds) with age. Calculated regression lines.

Righting Reaction

Each rat was held, back downwards, by its head and tail, and released from a height of 12 inches. Analysis of the mean age at which the rats of each group first succeeded in landing on their feet showed that the maturation of the response was significantly delayed in both starved and hypothyroid rats, but that the latter were the more severely affected (Table II*e*).

Placing Reaction

The rat's chin was touched against a horizontal bar and the first appearance of the response was recorded as the age at which the animal first placed both forepaws on the bar on either side of its chin. Tested by probit analysis, the results show that the maturation of the response was slightly retarded in the starved rats but severely so in the hypothyroid (Table II*f*).

Motor Co-ordination

Rats were trained to run for food in one direction along a spar one inch wide and eight feet long. When each rat could be relied upon to run immediately after being placed at one end, another spar was substituted which was one inch wide at the starting end but which tapered to a point at the reward end. This spar was graduated at six inch intervals in order to assess the point at which the narrowing of the rat's foothold caused changes in its behaviour. Five measures were used to assess the rats' performance:

(i) *Learning ability*—the mean number of trials required by the rats of each group to learn to run the non-tapering spar, expressed as the reciprocal (percentage) of the number of trials required by the quickest-learning rat.

(ii) *Success*—the percentage of the total number of trials in which the rats of each group reached the reward.

(iii) *Retraces*—the percentage of the total number of trials in which the rats did *not* retrace their steps during their forward progress.

(iv) *Point of hesitation*—the mean distance from the start which the rats' progress was retarded by the tapering of the spar, expressed as a percentage of the total length of the spar.

(v) *Point of stumbling*—the mean distance from the start at which the rats of each group lost their foothold, expressed as a percentage of the length of the spar.

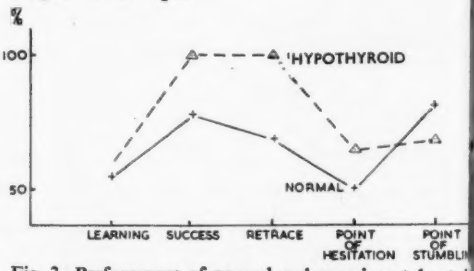
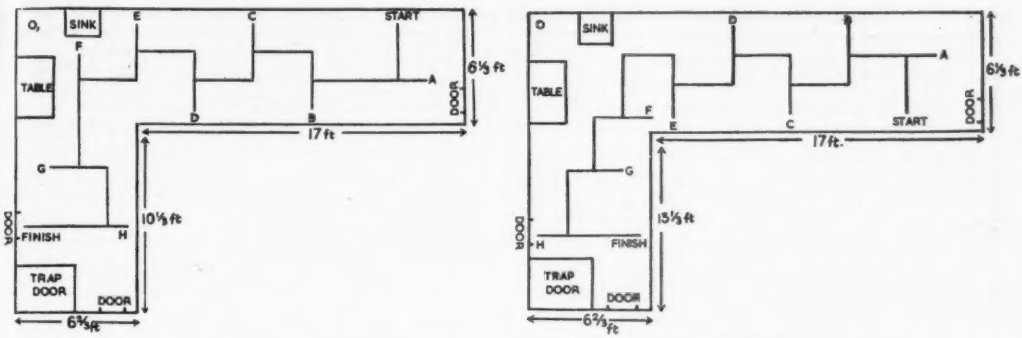


Fig. 3. Performance of normal and experimental rats in tapered spar test. For explanation see text.

The results, summarised in Fig. 3, show that the hypothyroid rat learned slightly more quickly than the normal. It always succeeded in reaching its goal; it never retraced its steps and its first point of hesitation was further along the spar than for the normal animal. On the other hand, it first lost its foothold at a point nearer the start, i.e., where the spar was wider than was the case with the normal rat. The experimental animals approached this point without slackening their speed of running whereas the control animals invariably hesitated in their progress along the tapering spar a short distance before actually losing their foothold.

Spatial Elevated T-maze

Two mazes of the type described by Mile (1930) were used. The design of each (Fig.



MAZE A MAZE B

Fig. 4. Arrangement of sections in elevated T-mazes A and B used to test learning ability of normal and experimental rats.

was governed by the available space, but attention was paid as far as possible to the accepted criteria for a maze of high reliability (Kreezer, 1942). Correlation between errors made during odd and even trials gave reliability coefficients of 0.82 for Maze A and of 0.93 for Maze B. Each rat was motivated by reducing its food to two-thirds of its normal intake, and was tested once daily on one or other of the mazes. Two preliminary and unrecorded trial runs were given on Maze A to build up the association of the maze with food and thereafter records were kept of:

(i) the time taken to reach the reward,
(ii) the number of errors (i.e. blinds entered and retraces away from the goal),
(iii) the number of trials required to learn the maze to the criterion of three successive correct runs, or four successful out of five consecutive runs.

When each rat had successfully learned Maze A it was, on the following day, transferred to Maze B where similar observations were made.

The results (Table III and Fig. 5) show that both cretinoid rats given thyroxin and rats which had been starved during infancy, performed in all respects as well as their normal controls. On the other hand, the untreated hypothyroid rats took on the average longer to run each maze and made a significantly greater number of errors than those of the other groups. They were not, however, greatly inferior in the number of trials required to learn the mazes. The performance of all classes of rat on Maze B was significantly better than that on Maze A ($P < 0.01$).

The three measures of performance used in this experiment are clearly interdependent, and the data were accordingly analysed further in an attempt to determine how far the greatly increased time taken by the hypothyroid rat to learn each maze was attributable to a slow rate of locomotion and how far to time lost as a result of its increased number of errors. Accordingly, the mean time taken by each rat for its last three correct runs was regarded as an index of its characteristic speed of locomotion, an assumption which was justified by the fact that the times taken by all groups for correct runs on Maze A were almost identical with those taken on Maze B. Statistical analysis of these times (Table III) showed that hypothyroid rats moved significantly more slowly than those of the other three groups, whereas estimation of the mean time wasted per error* showed that the hypothyroid rats were conspicuously less delayed by each error than were the other classes of animal. Significantly less time was lost per error on Maze B than on Maze A.

It must be inferred that the poorer performance of the hypothyroid rat is due partly to its slower rate of progress along the maze, and partly to the fact that it makes more errors than the normal.

Three-Table Test

This test was originally devised by Maier (1932) to test a capacity "higher than learning" which he termed "reasoning." The structure of

*Calculated from the formula $\frac{T_1 - tT_2}{E}$ where

T_1—total time to learn maze
T_2—mean time taken for errorless run
t—total number of trials to learn maze
E—total number of errors made during learning.

TABLE III. Performance of Normal and Experimental Rats on Elevated Spatial T-maze

Measure of performance	Maze	Group 1 Normal*	Group 2 Starved/ re-fed*	Group 3 Hypothyroid	Group 4 Hypothyroid/ thyroxin*
Number of trials to learn	A	16·5	17·6	17·9	11·9
	B	12·1	9·0	13·6	8·1
	Total:	28·6	26·6	31·5	20·0
Numbers of errors made during learning	A	22·8	29·4	40·6	20·8
	B	17·9	10·3	22·6	9·8
	Total:	40·7	39·7	63·2†	30·6
Time taken to learn (mins.)	A	20·8	23·3	34·2	17·3
	B	12·8	8·2	20·7	9·5
	Total:	33·6	31·5	54·9‡	26·8
Mean time taken for correct run (secs.)	A	39·2	43·8	69·0	44·9
	B	45·8	40·6	70·1	39·1
	Total:	85·0	84·4	139·1‡	84·0
Mean time lost per error (secs.)	A	30·5	20·0	15·3	23·0
	B	10·3	17·3	12·3	19·0
	Total:	40·8	37·4	27·6	42·0

*In no instance was there any significant difference between normal, starved/re-fed and thyroxin treated hypothyroid groups. ‡Differs significantly from other groups (P=0·02–0·01). †Differs significantly from other groups (P<0·01).

TABLE IV. Relative Success of Normal and Experimental Rats In Solving 3-table Problem

Class of rats	No. of rats	Choices		Success Index*	Statistical significance
		Correct	Incorrect		
Normal	4	44	16	46·7%	0<0·001
Starved/re-fed	4	30	30	0%	P>0·9
Medicated hypothyroid	3	23	22	17%	

* This index, defined by Maier (1934), is the difference between correct and incorrect responses expressed as a percentage of the total number of responses. The index expected of a rat unable to solve the problem will therefore be zero.

the apparatus, mode of conduct of the experiment and scoring of the results were as described by Hanson (1949). Eleven rats, aged 60 days at the start of the tests, were used (four normal, four starved and re-fed, and three given methyl thiouracil during infancy).

The results (Table IV) show that only the normal animals performed the test successfully, the number of correct and incorrect choices made by both the experimental groups being such as might be expected as a result either of random selection of the two alternative pathways or to the systematic choice of one of them (e.g. the right or left in relation to the line of advance).

Discussion

The precise interpretation of the tests of innate behaviour is complicated by the fact that each test probably measures more than one aspect

of maturation. For instance, at least three factors could be invoked to explain the changes in the threshold for reaction to peripheral stimulation —the conductivity of the skin, the excitability of the conducting pathway and the level of central facilitation in the synaptic zone—and there is at present insufficient evidence to assess the contribution made by each. Four of the tests, however, may confidently be accepted as measuring in some part the maturation of central nervous mechanisms. The progressive changes in the form of response to pinching the tail (Tilney, 1933) undoubtedly reflect the increasing dominance of suprasegmental centres during the course of central nervous development, and the same may be said of the increase in suspension time (McGraw, 1943). The righting and placing reactions depend upon the integrity of mesencephalic and cortical centres (Rademaker, 1931; Brooks, 1933) respectively, and so presumably owe their appearance to the functional maturation of these centres. We can conclude, therefore, from those results which deal with the appearance of simple and automatic forms of innately organised behaviour that in the rat, as in man (Gesell, Amatruda & Culotta, 1936) the maturation of the central nervous system is retarded as a result of thyroid deficiency. The similar retardation which follows early inanition (Biel, 1939), however, seems to apply to certain patterns of behaviour only, for the starved rats in the present experiment did not differ significantly from their normal littermates either in their response to compressing the tail or in the duration of reflex suspension. In no instance was the effect of starvation on neural maturation as severe as that of hypothyroidism.

Thyroid deficiency begun during infancy was also responsible for changes in adaptive behaviour which can best be explained in terms of a reduced sensitivity to the external environment. Thus, in the tapered board test, where the problem is a simple one, and habituation to a new situation plays a large part in its solution, the hypothyroid rat performs better than the normal. Not only does it learn more quickly to run in a given direction, but fails to perceive a newly introduced obstacle and, in spite of the handicap of poor motor co-ordination, persists in the completion of an established habit where the normal rat will hesitate. On the maze, however, where habituation plays a relatively smaller part in the process of learning, the hypothyroid rat is inferior to the normal, but even here, the fact that it loses less time over each error suggests that it is less inhibited by encountering an unexpected situation. It seems, therefore, that a reduced sensitivity to its surroundings, while enabling the cretinoid individual to habituate readily to a new environment, reduces its capacity to solve a more complex problem.

Previous attempts to determine the effect of thyroid deficiency on learning ability have given inconsistent results. Rockwell (1931) was unable to find that thyroidectomy during adult life had any effect on maze learning, while others have concluded that this procedure is without effect either on the retention of a learned response (Burnham, 1940; Burnham & Leonard, 1941), or on relearning (Brody, 1942). On the other hand, both Rickey (1925) and Carlson (1941) found that the capacity to learn a maze was reduced after thyroidectomy, Carlson showing that the major decrement in performance was in the time scores. The results of the present experiment support this view, and in addition suggest that the age at which thyroidectomy is carried out is a factor which determines the subsequent learning ability of the untreated hypothyroid animal.

Although it is thus clear that cerebral function in the rat is impaired as a result of early hypothyroidism, the improvement in the maze-running ability of the thyroxin-treated hypothyroid animals is similar to that of rats thyroidectomised during adult life and later given thyroid substance (Rickey, 1925; Watanabe & Nomura, 1936; Carlson, 1941). The age at which the animal was thyroidectomised would, therefore, seem to have little bearing on the degree of recovery resulting from replacement therapy. In this respect, the cretinoid rat resembles the rat starved during infancy and subsequently re-fed, for both in the present experiment and in earlier work reported by Biel (1938, 1939) such rats learned a maze as readily as did normal animals.

We can only speculate about the way in which these results help us to interpret the variable effects of replacement therapy in the human cretin. In the first place it must be noted that, although the maturation of automatic behaviour was grossly retarded in the hypothyroid animal, none of the patterns of behaviour that were studied failed eventually to appear. Secondly, the cerebral changes caused by thyroid deficiency whether measured in terms of the histology of the cerebral cortex (Horn, 1954) or, as in the present experiment, of behavioural indices,

are not permanent, but can be reversed by giving thyroid hormone. And finally, the effects of starvation both on the structure of the cerebral cortex, and on behaviour, although not identical with those of hypothyroidism, are similar in trend, and so suggest that the changes due to a deficiency of thyroid hormone may not be attributable to a selective effect of the hormone on nervous tissues. In so far, then, as our findings may be held to relate to the corresponding condition in man, they support the view that the irreversible cerebral changes found in many cretins are not due to an uncomplicated thyroid deficiency but to the co-existence of some additional, and probably congenital abnormality. Conclusions in this respect can only be tentative, however, for the functional capacity of the human brain far exceeds that of the rat, and we do not yet know how far early thyroid deficiency may affect the maturation of the mechanisms underlying such processes as fall outside the range of the rat's capability.

Summary

1. Rats made hypothyroid during infancy, either by radio-thyroidectomy or by giving daily doses of methyl thiouracil, have been subjected to a series of tests designed to measure the maturation of innately organised behaviour and the capacity to respond adaptively to a new environment. Rats starved during infancy have been similarly treated.

2. Both the hypothyroid and starved rats matured more slowly than untreated littermates during the first 24 days of life, but the effect of thyroid deficiency was significantly more severe than that of starvation. Later in life, non-medicated cretinoid animals, although apparently becoming habituated more readily to a new situation than normal littermates, performed less well on an elevated spatial T-maze.

3. Rats starved during infancy but subsequently given ample food, and thyroxin-treated cretinoid rats, performed on the maze at least as well as did normal animals.

4. The significance of these results, and their contribution towards an explanation of the irreversibility of cerebral defects in many human cretins, is discussed.

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THE DISCRIMINATION BY THE NOSE OF THE DOG OF INDIVIDUAL HUMAN ODOURS AND IN PARTICULAR OF THE ODOURS OF TWINS

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Francis Galton's suggestion (1875) that "it would be an interesting experiment for twins who were closely alike to try how far dogs can distinguish between them by scent," has to the author's knowledge never been put to any deliberate experimental test. What evidence exists on this point, has arisen from chance observation and points to the conclusion that dogs may not be able to distinguish between the body odours of identical twins. For instance, in a letter dated 15th October, 1952, from Mrs. John W. MacArthur to Professor Penrose, the following experience which was brought to the knowledge of the late John W. MacArthur, Professor of Genetics of Toronto University, is recorded:

"In a prospector's camp in Northern Ontario was a nearly blind great dane, Silva. She was not a friendly dog, but she had a passion for one prospector and fawned on him delightedly whenever he came to camp.

One day a stranger appeared for the first time and to the surprise of those present, Silva greeted him with great affection. Upon enquiry by the camp crew it was found that the stranger was the identical twin of the particular prospector, whom Silva had such a passion for, and that he had never been there before nor seen the dog before."

The fact that a dog can pick out an individual from others may appear commonplace but for the fact that recently there are indications that sweats may be as different and as characteristic genetically as bloods and salivas (Penrose, 1953). In phenylketonuria, for instance, abnormal substances are found in the sweat (Jervis, 1950) which are believed to give it a characteristic smell.

In the present paper controlled experiments are described, concerning the discriminatory powers of dogs' noses and, in particular, their limited ability to distinguish between the body odours of twins.

Discrimination of People Other Than Identical Twins

If confusion by a dog of the odours of identical twins is to be taken as proof of the exceptionally high chemical similarity between the twin partners, it must first be established that the same dog can discriminate with ease and reliability between the body odours of people who are not identical twins, i.e., between unrelated people, and members of one family. The first task was thus to select good dogs and to explore the conditions under which they can work successfully. According to their training two types of dogs were found and two different types of experiments were gradually developed, namely retrieving, which was performed either indoors or in the open, and outdoor tracking, of which there were two schemes; this will be described later.

The nine dogs used in these experiments varied greatly in intelligence, perseverance and the degree to which they had been trained. Four were young male Alsatians trained for police duty by individual police officers; one male Doberman Pincher and an old male Labrador were also police dogs, and there was one bitch, a German Pointer (Jagdhund), who however, was "multihandled," i.e., she could be made to work by several people. The two other bitches used, both Alsatian and several years old, were show dogs and particularly good at retrieving.

Seventeen men, nine women and five children were used in these experiments, all of whom were Europeans with the exception of one male African. The task was either to single out a handkerchief scented by a particular person or to find a track laid by a particular person among tracks laid by four to ten others.

The task of finding a particular human individual, or a track, or a scented object, is given to the dog by its human handler and the problem is solved by the co-operation of the two. The first precaution in experiments concerning discrimination by a dog's nose must thus be that the person who handles the dog should not know the answer to the problem and should have no preference for any particular solution; in this respect animal psychologists and police have to be particularly careful. Löhner (1924) describes how a trained goat seemed to learn individual human scents with great ease, but failed completely as soon as its

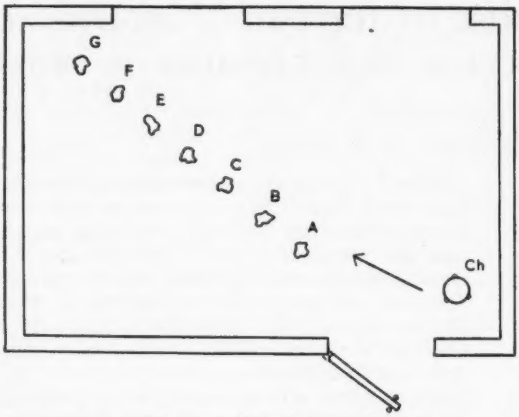

Fig. 1. A row of handkerchiefs (A-G) laid out in a room for retrieving. The person whose body odour is sought for sits in the chair, Ch.; the dog is led in by the door, made to sniff the person's hands and sent off in the direction of the arrow.

owner did not know the correct answer. In the present experiments dog and man were never at the site while scented objects were laid out or tracks were being laid.

The limitations of a dog's understanding, although varying a great deal, nevertheless imposed a severe restraint on experimentation. Thus, on most occasions the dog had to be gradually and repeatedly taught its task, proceeding from the simpler to the more difficult (see experiment on p. 29), and it was also patted or rewarded when successful and discouraged after failures.

Only an exceptional dog can, during any one experimental session, change from searching for one person's odour to searching for another's odour. Thus experiments were as a rule so arranged that only one odour was tried on any half day on one dog. There was little sign of "nose fatigue" in the experiments, but after one hour or so most dogs lost interest and their performance became erratic. It was then little use to persevere with the experiment.

Retrieving Experiments

These were a version of the retrieving tests usual at dog shows. The procedure was as follows: first, a number of marked handkerchiefs,* one of which was scented for a few minutes in a person's armpit, were laid out in a straight line in the absence of dog and handler. These were then called in and the dog made to sit down; it's muzzle was then clasped for about half a minute by the hands of the person who had scented the handkerchief. Indoors (Fig. 1), the dog was commanded to walk over the handkerchiefs and to seek and bring back the scented one. Outdoors (Fig. 2), the dog was sent obliquely against the wind and at a slight angle to the row of handkerchiefs. Usually the dog brought back the scented handkerchief at the first attempt but sometimes it overshot and only brought it back when returning or at a second attempt. In any case, the next step in the experiment was only taken after success in this task. This second step consisted of asking the dog to pick out the "right" handkerchief not among a row of unscented ones (blanks) but among handkerchiefs scented in the armpits of other people.

The results of several such experiments indicated that although there was some variation in the day-to-day performances of some individual dogs, nevertheless a few dogs were very sure in retrieving. These were subsequently used in the twin experiments.

Tracking Experiments

These were performed in two different ways. The first type (Fig. 3) of tracking consisted of a number of people walking into a field side by side for about 100 yards, where one of them dropped a handkerchief, glove, cap or similar object. After a further 25 yards or so the people fanned out and when they reached a distant hedge or a row of trees, either hid behind the hedge or climbed the trees so that they were not visible from the field. The dog was then led

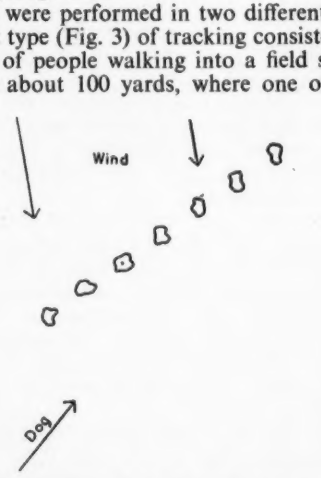

Fig. 2. A row of handkerchiefs laid out in the open.

*Three dozen handkerchiefs were washed, ironed and stored for a few days before every experiment by a person not taking part in the experiments. They were then handled by means of plastic forceps.

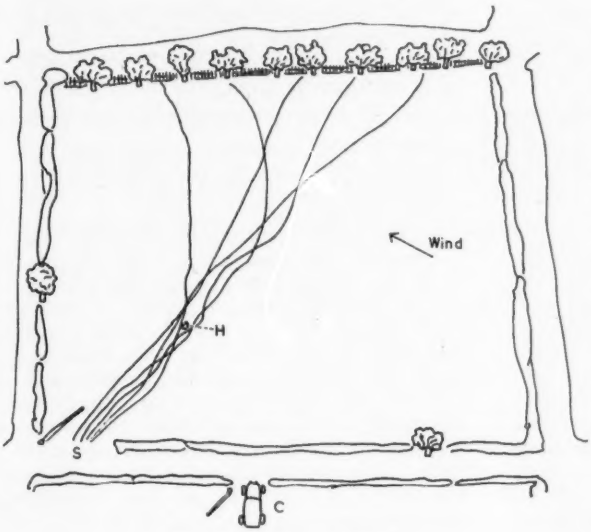

Fig. 3. Fanning out tracks.

from the car C to the point where the men had entered the field, and put on the scent on a tracking line. He picked up the dropped object and followed one track, and it was then ascertained whether he had followed the right one. A new field had to be used for each such experiment and the direction of the wind had to be taken into account as direct air scent interferes with the tracking. The outcome of these experiments was that those police dogs, which were advanced in their training, were quite reliable in picking out the correct track among a number of incorrect ones.

The second type of tracking experiments followed the design given by Budgett (Fig. 4). A person walked from the lee side (1) into a field until he reached a point P where he stuck a pole or branch into the ground and also dropped an object at 2. He then walked on at an angle until he reached the hedge at 3 and continued behind it to 4, where he hid. Another person starting from the same point 1 passed the pole and the dropped object and continued towards 5 and 6; after returning to P he walked towards 7 and 8, returning to P for a second time, then proceeded to the hedge at point 9, i.e., opposite the first person, and finally hid at 10. The handler and a dog on a tracking line were then summoned from the car C to position 1 and the dog put on the track. The dog picked up the dropped object, which the handler took from him and later gave it back to him to sniff. In the neighbourhood of P the dog had a choice of 5 tracks by the second person and one track of the first (to whom the object belonged), and it was then seen whether he followed the correct track or one of the five wrong ones. Table I shows that Kim, a well trained Police dog, made very few mistakes when the two people laying the tracks were not identical twins.

Twin Experiments

Retrieving and tracking were used in the experiments with different results. Four pairs of apparently identical twins were tested, three female and one male. Previous experience makes it very improbable that the body odours of fraternal twins would be more similar than the body odours of sibs of different age; none were so far tested.

One retrieving experiment is described in some detail: Two identical twin sisters, (T_1 and T_2), aged 14, their sister (S) aged 12, their father (F) all living in one household, as well as four non-related people (P, K, L, R,) were

Table I. Budgett's Layout

Name of Dog	Sex	Age	Breed	Follows correct track from	Follows one wrong track from	Remarks
Kim	M	18 mos.	Alsatian	6 6		Follows wrong track for about 50 yds. then casts back and finds correct person.
Kim	M	18 mos.	Alsatian	6 6		
Kim	M	18 mos.	Alsatian	6		

tested in a room in the fashion illustrated in Fig. 1. The twin sisters were extremely similar in every respect. The blood antigens of the family were:

Father (F)	O	MsMs	rr	P+	Le(a+)	K—	Lu(a—)	Fy(a+)
Mother	A_2B	N S	rr	P+	Le(a—)	K—	Lu(a—)	Fy(a—)
Twin sisters (T_1 & T_2)	A_2	MNS	rr	P—	Le(a—)	K—	Lu(a—)	Fy(a+)
Sister (S)	B	MNS	rr	P+	Le(a+)	K—	Lu(a—)	Fy(a+)

A fresh handkerchief was put for 10 minutes in T_1's armpit and then laid 4th in a row of handkerchiefs as follows, B B B T_1 B, where B means unscented blanks. The dog Chloë, a three year old Alsatian bitch, was then led into the room and T_1 put both hands for half a minute over her muzzle. She was then commanded to walk over the handkerchiefs and to seek and bring back the scented one. She first played about, but when again commanded to retrieve, brought back the correct handkerchief and was patted. Chloë was led out of the

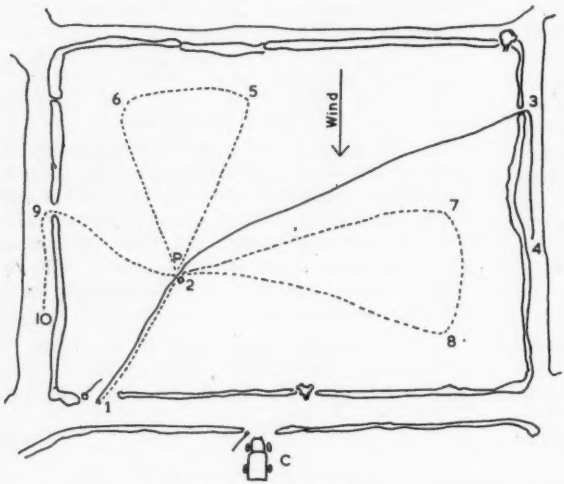

Fig. 4. Budgett's layout.

room and the same handkerchiefs were laid out in the sequence B B T_1 B B.* She was now immediately successful and was patted.

Next, a handkerchief, scented in the armpit of the second twin T_2 was placed among four blanks in the order B T_2 B B B. Chloë, when led in, sniffed the hands of T_1; sent out, she brought back T_2 without hesitation. She was not patted on this occasion. It was now considered that Chloë understood the situation. She was clearly able to pick out a handkerchief scented by T_1 from among blanks and she also retrieved T_2 instead. The significance of the acceptance of T_2 for T_1 was then assessed by offering T_1 and T_2, or both, among a number of handkerchiefs scented by other people. Using the same procedure as before, Chloë, after sniffing T_1's hand was confronted with the sequence S L K T_1 P R F. She playfully picked up S, the first one belonging to T_1's younger sister, then dropped it and retrieved T_1. She was patted and given a biscuit. The experiment was repeated with the sequence F S P T_1 L R and was immediately successful.

Now T_2's handkerchief was put into the sequence F S P L T_2 R, from which T_1 was missing. T_1's hand was sniffed, but T_2's handkerchief was retrieved without hesitation. This time Chloë was patted and rewarded. The experiment was then repeated with the sequence P S T_2 L R F and Chloë again retrieved T_2. In a second repetition Chloë overshot T_2 in the sequence S R F T_2 P L, but when she turned back and worked the handkerchiefs from the far end, she picked up T_2 and brought it back. She was patted and rewarded. At this stage it was concluded that Chloë accepted, in the absence of the "correct" scent and from a sample of body odours containing those of a younger sister and her father, as well as non-related people, only the body odour of her monozygotic twin sister.

The next experiments were designed to show whether, when the body odours of both twin sisters were in the series, a preference for the correct one could be detected. First, T_1 and T_2 were offered among unscented handkerchiefs (blanks). Working the series B B T_2 T_1 B B Chloë retrieved T_2, which was the first she came across, and after this was removed, and the row rearranged closing the gap, she retrieved T_1 when led in again. No difference in the certainty of reaction or in any other way was observed.

* Persons and handkerchiefs scented by them are denoted by the same letter.

For the next experiments the handkerchiefs, scented by the twins were laid out among six handkerchiefs, scented by their father, sister and four non-related people, in the following sequence: R K S T_2 F T_1 P L. Chloë, after sniffing T_1's hands, retrieved T_2 which was first on her way without hesitation, and after its removal and the rearrangement of the rest she retrieved T_1, again without any observable difference in behaviour. An interval of 10 minutes ensued, during which Chloë was fed and given water. A training run was put in, in which Chloë successfully picked out T_1's handkerchief among seven handkerchiefs, none of which were scented by T_2. Finally, the sequence P T_1 S K T_2 L F R was offered Chloë; she overran T_1 and retrieved T_2, and when the gap was closed and she was sent out again she retrieved T_1.

The conclusion from this series of experiments is that in the circumstances stated Chloë accepted the identical twin sister's body odour for the original one and, when offered handkerchiefs from both among several scented with other people's body odours, indiscriminately retrieved that which she first came across. The dog did not seem to prefer the scent of either a younger sister or the father of the twin, to the odour to which she had been trained.

A similar set of experiments was performed with two identical twin sisters, aged 23, both post-graduate students living together. Their blood antigens were as follows:
O MsNs R_1R_1 P+ Le (a–b+) K–Lu (a+) Fy(a+)

The same dog was used. The results are summarised below:

The results of tracking experiments, while also indicative of a great similarity between the odours of identical twins, nevertheless suggested, that in this situation good dogs might be able to distinguish by smell between identical twin partners. Budgett's layout (Fig. 4) was used for each experiment, and a new field for every set of tracks. The results of two such experiments were as follows:

26th December, a cold day with wind and drizzle. The two identical twins, married men aged 33 who had lived in different places for several years, had the following blood antigens in common:

A_1 NsNs Ror P+ Le(a–) K– Lu(a–) Fy(a–).

A Police dog Kim, an Alsatian male aged 18 months, was used. In two preliminary tests, Kim twice picked out the track of one of the twins from five tracks of an unrelated person. He was next set on the double tracks made by the twin brothers. After picking up a glove of the twin brother, used in the preliminary experiment, he unhesitatingly followed his track, although it bent on the crossing point and there were five tracks laid by the other twin brother. When the experiment was repeated in a new field, Kim followed the right track for about 50 yards but then lost it, presumably owing to the strong wind. Casting about he found it again and followed it to where it left the field through the hedge (point 3). Here, however, Kim lost the track again, and when led back to the starting point, he got confused and followed several of the false tracks. The experiment was then repeated on new tracks laid in a fresh field. The force of the wind had by then in-

Sequence	Chloë, after sniffing T_1's hand, retrieved	
B B T_1 B B	T_1	Patted
B T_1 B B B	T_1	Fed on biscuit
B B B T_2 B	T_2	
R P T_1 O H	T_1	patted
K O R P T_1 H	T_1	patted, fed on biscuit
H P R O T_2 K	T_2	after overrunning and working back
O J T_2 K R T_1 P H	T_2	which is first in the way
O J K R T_1 P H	T_1	
H T_2 J B K R T_1 P O	T_2	
H J B K R T_1 P O		Refusal to bring any handkerchief back. Second try
H J B K R T_1 P O	T_1	
10 minutes pause, while fresh handkerchiefs were scented in all armpits for 5 minutes.		
W T_2 R P T_1 L M	M	The last one brought back. Failure! Chloë scolded
W T_2 R P T_1 L	T_2	
W R P T_1 K L	T_1	Chloë patted
P L T_2 N T_1 R W	T_2	
P L N T_1 R W	T_1	

creased to such an extent that Kim tracked about two yards to the lee side of the tracks, and in this way after some time on the right track he got onto one of the false ones. Finally, the air scent of the "correct" twin was picked up and Kim ran to him directly, i.e., not following any track, and barked at him. Bad weather made continuation of the experiment impossible.

31st January, a frosty, but sunny, day. Two identical twin sisters aged 32, unmarried and living in one household, having the following blood antigens in common:

O MsMs R_1r P+ Le(a–) K– Lu(a–) Fy (a+)

A male Alsatian Kim, 19 months old was used.

In a preliminary experiment, Kim picked up the handkerchief of one twin and followed her track among five other tracks of an unrelated person. In the next experiment, the handkerchief scented by the first twin sister was deposited at P by the unrelated person, who also laid the five tracks, and the single track was laid by the second twin sister. Kim picked up the handkerchief of the first twin and followed the track of the second twin for most of the way, in preference to the five tracks of the unrelated person. At the very end, Kim picked up the air scent from the first twin and running to her barked. In a new field the first twin sister dropped her handkerchief and laid the single track, while the second laid the five fold track. Kim picked up the handkerchief and followed the track of the first (=correct) sister. He did so again, when the experiment was repeated in a new field.

After this experiment the dog, walking between the two sisters got somewhat excited and presumably confused. When given the handkerchief of the first twin to smell at and asked to "speak," he sniffed at both girls several times and finally barked at the first (=the right) one.

From these experiments one might conclude that Kim accepts in the conditions stated, i.e. mainly in the absence of the correct odour, the odour of an identical twin sister, but that when both odours are available he is able to discriminate between them.

Discussion

The above statement may also explain why some tracking experiments revealed the power of the highly trained canine nose for discriminating between the body odours of identical twin partners, whereas the retrieving experiments did not reveal any sign of this. The difference is very likely to be found in the variation between the situations in the two types of experiments. A tracking dog, casting about is more or less simultaneously confronted with a mixture of the odours of the two twin partners and can pick out the right one, but a retrieving dog sniffing at each handkerchief in turn, is at any particular moment confronted with one odour only. If this is sufficiently similar to the one remembered, the dog retrieves. The situation may be likened to visual recognition if one considers that one might easily pick out one identical twin from among a group of people, when shown the photograph of the other, but that when both partners are simultaneously available, their distinction becomes quite feasible.

It would be tempting to suppose that scent discrimination between different people must be based on differences between complex mixtures of a number of chemical substances, and that it would be more of a quantitative than of a qualitative nature. Differences in the odour of bees from various colonies have been recently shown (Ribbands & Kalmus, 1952) to be dependent on diet and thus are presumably of this nature. However, several observations exist which are difficult to reconcile with the assumption that the scent discrimination by dogs depend solely on quantitative differences. (1) As shown previously (Löhner) as well as in the above experiments, regional differences in body odours of one person, e.g., those between the arm pits, the palms and the soles, though markedly different for the human nose, do not prevent the dog from recognising that they all belong to the same individual and from distinguishing them from the body odours of others. (2) Evidence for this point of view also comes from an old observation by Romanes (1885), and an experiment described below.

Romanes describes how he took his terrier to Regent's Park on a Bank holiday, when the Broad Walk was swarming with people. When the terrier's attention was diverted by a strange dog, Romanes suddenly made a number of zig-zags across the Walk, then stood on a seat and watched the terrier picking up his scent and tracking his footsteps over all the zig-zags he had made until it found him. In order to do this it had to distinguish it's master's trail from at least a hundred others quite as fresh, and many thousands of others not so fresh, crossing it at all angles.

This observation is paralleled by the following

experiment. Gretchen, an 8-year-old Alsatian bitch, had learned to pick out one person's handkerchief in the manner illustrated in Fig. 1. She was then offered a handkerchief among others scented in the armpit of this particular person as well as in the armpit of another person, also represented by herself among the other handkerchiefs. In two experiments the bitch nevertheless twice picked out the doubly-scented handkerchief. She also picked out the correct handkerchief when the armpit smell was overlaid (for the human nose at least) with the smell of Collidine, or pentadecanoline.

The role of environmental factors in the origin of individual odour differences, e.g., of diet, clothing, or personal hygiene, is difficult to assess, and, apparently, as long as one deals with healthy people it is not very great, but it seems sufficient to enable a well trained dog under optimal experimental conditions to distinguish between some twin partners, who were to all appearances identical.

On the other hand twin partners were the only people observed, whose scents in different circumstances could consistently be substituted for each other without the dogs' noticing it.

From all this one might tentatively conclude that the volatile substances responsible for the discrimination by dogs of individual odour differences are the result of numerous innate metabolic differences, and that this chemical aspect of human individuality is possibly based on polyallelic differences in several chromosome loci.

Summary

Controlled experiments are described showing that Police dogs trained to follow human tracks, and show dogs trained to retrieve objects scented by people, can distinguish fairly reliably between the body odours of different individuals, including the members of a family. The individuality of a person's body odour as perceived by the dog's nose is not greatly dependent on the region (e.g. palm, armpit, sole) from which it emanates, although these regional odours appear quite different to the human nose. The individual odour of a person is perceived by the dog even when mixed with another person's body odour, or with some strongly smelling substances.

In retrieving experiments the body odours of identical twin partners offered in succession are accepted for each other and there is no indication that the dogs perceive any difference.

In tracking experiments in which two body odours are offered simultaneously and mixed up, those of identical twin partners are distinguished by the dogs. However, when the odour of one twin is offered in place of the odour of the partner, and in the latter's absence, it is picked out from the odours of other people. Thus, the odours of identical twin partners, although more similar than those of any other people tested, can nevertheless be distinguished by well trained dogs.

Acknowledgments

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Last, but not least, I must thank the numerous participants in the experiments.

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NOTE ON THE COURTSHIP AND PREDACEOUS BEHAVIOUR OF *Poecilobothrus nobilitatus* L. (Dipt. Dolichopodidae).

By KENNETH G. V. SMITH* and D. W. EMPSON
Entomology Department, N.A.A.S., Woodthorne, Wolverhampton.

Little has been recorded of the behaviour of adult Diptera although the predaceous species have received more attention than others. The Dolichopodidae are recognised as one of the predaceous Dipterous families, but there have been few detailed studies of the nature of the prey. Several species of Dolichopodidae along with certain Empididae and Ephydridae inhabit the surface film and feed on the animals caught therein. Laurence (1952) summarises our knowledge of these species and among the Dolichopodidae possessing this habit he refers to *Hydrophorus* and *Campsicnemus*. Some Dolichopodids will also feed on truly aquatic larvae. Williams (1933: 307) has observed *Hydrophorus pacificus* V.D. in Hawaii pulling *Chironomus* larvae out of shallow water along muddy shores and in marshes (*vide* also Clausen, 1940: 383). In England Parmenter (1950: 114) records a male *Dolichopus ungulatus* L. with a Chironomid larva as prey.

The courtship behaviour of Dolichopodidae is interesting in that the males of many species have special characters developed ornamentally for use in display, Van Duzee, Cole and Aldrich (1921: 2) described these characters and their use in courtship as observed in five American species. In *Dolichopus tenuipes* Aldrich the fore tarsi of the male are elongated and slender, with the last joint in the shape of a comparatively large, oval black disc. These are moved up and down in courtship display. In *Dolichopus crenatus* O.S. the antennae are modified, being large and covered with black pubescence. During courtship the male hovers before the female displaying these antennae to the best advantage.

Poecilobothrus nobilitatus L. is a fairly common British species. The males are readily identifiable by the whiteness of the wing-tips. The observations here recorded were made during the afternoons of July 22nd and 27th at Chorley covert in south-east Shropshire, the flies being fairly common in sunshine at water filled cart ruts along the woodland rides. Activity died down and gradually ceased when the sun was obscured, the flies retiring to nearby herbage.

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Hunting

On only one occasion was a capture seen, but the method of hunting was quite plain. The flies settle on the surface of the water and then make a series of short flights of about three to six inches over the water, settling on the surface of the water after each flight. On the occasion mentioned above a female alighted directly over a last instar larva of *Culex pipiens* which was at the surface taking air. The larva was attacked, probably with the fly's mouthparts and after a short struggle was carried on the wing to the mud at the side of the cart rut. Although larvae and pupae of *Culex* were plentiful in the water the flies did not appear to be searching for them. They seemed to alight at random and the capture was made on the only occasion a *Culex* larva happened to be close. Frequently a fly would alight within an inch or so of a *Culex* larva at the surface without apparently noticing it.

The activity was most common in the females although at times it was observed in the males. The latter sex, however, was mostly engaged in either courtship or fighting. The *Culex* larvae were identified by subsequent breeding of adults.

Courtship

The females took no obvious part in the courtship display observed here except to terminate activities by flying away. Courtship was mainly performed on the mud banks and only rarely was it attempted on the surface of the water.

On the approach of, or after alighting close to, a fly of the same species, the male first raised its wings slightly. This occurred when the insects were about three inches apart. If the second fly was also a male it sometimes turned towards the first and raised its wings whereupon the two would fly together and fight until one was driven off, usually almost at once. If the second fly made no movement the first walked towards its side, staying about two inches away from it. Males approached in this way turned

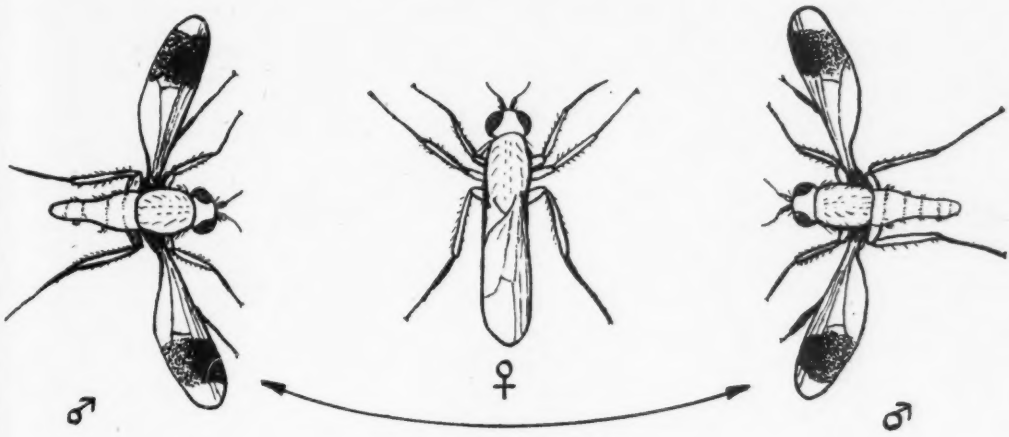

Fig. 1. Slow display flight.

to face the first fly and were attacked by it and driven off; females remained still with their wings folded normally, over the back. The next stage was a display by the male as it approached to within one inch of the side of the female. Its wings were raised and lowered together rather in the manner normal to Sepsid flies, but at about twice the rate. The white wing tips were very conspicuous during these wing movements. If the female did not move, the male then made two or three short curved flights *behind* the female, pausing to repeat this display on each side of the female (Fig. 1). Then three or four very rapid consecutive flights directly over the female completed the display (Fig. 2). There were no pauses for the wing-wagging display during these rapid flights; the male seemed to bounce from side to side of the female. No females were seen to respond to this display in any way and none of the pairs copulated. It is interesting to note that Van Duzee, Cole and Aldrich did not observe copulation in the species they studied although the male of *Dolichopus tenuipes* Aldrich were seen attempting without success to alight on the female's back. Wing movements were observed by these authors, but the males approached the females from the front in order to display the modified tarsi or antennae. The white wing tips seem to be the main factor influencing the different attitude observed in *Poecilobothrus*. At any one time during display the male fly would only be seen by one eye of the female. The slow flights from side to side would affect each eye alternately. The angle at which the wings are held combined with the relative

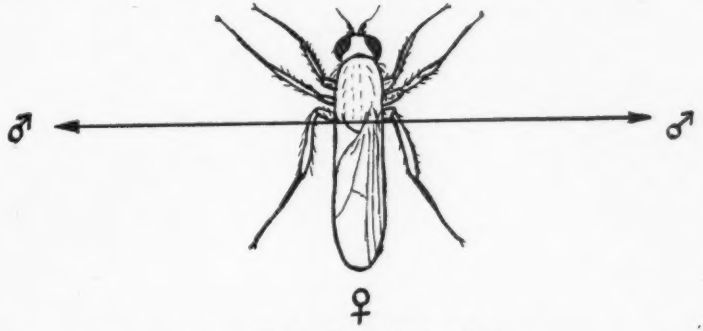

Fig. 2. Rapid display flight.

position of the two insects ensures that the white wing tips are presented to the compound eyes of the female in the most efficient way. If display were carried out in front of the female fewer facets of the compound eye would be affected by the wing movements.

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

At an Ordinary Meeting of the Association held in the Psychology Department, Birkbeck College, Malet Street, London, on Tuesday, 6th July, 1954, the following papers were read. The President, Dr. A. Walton, was in the Chair.

VOCAL COMMUNICATION IN THE CHAFFINCH, *Fringilla Coelebs*

By P. MARLER

Department of Zoology, Cambridge

An attempt has been made to study the communicatory function of the whole vocabulary of the Chaffinch, as part of an intensive field study. The theoretical approach embodies some ideas of elementary communication theory. For each of the twelve main calls, sub-classified in various ways, a list has been drawn up of all the characteristics and changes of the environment, external and internal—as far as these can be inferred from the observation of behaviour—that are always associated with the act of calling. By reason of the correlation the call may be regarded as containing potential information about these environmental factors.

By observing the response of each class of hearer, and referring to the other contexts in which that response is given, it is possible to deduce which of the items of potential information have been acted upon. For example, a reproductive male intruding into the territory of a male giving song, may act upon six of the nine items of potential information that have been listed for this particular vocalisation.

Some relationship can be found between the structure of a note and its information content. For example, certain notes used by the Chaffinch and other species in response to predators, appear to give a minimum of clues as to the location of the caller in space. Others, such as song, give a wealth of location clues which connects with the abundance of intra-specific, social information that song conveys. The possibility of confusion with notes of other species may be an important limitation on note form, as may be inferred from the increased variability of the songs of birds in the limited faunas of small islands.

The information transmitted falls into four categories. "Identificatory" concerns the identity of the caller as to species, sex, individual, etc. "Locative" concerns the location of the caller in space and time. "Emotive" concerns the motivational state of the caller. "Environmental" concerns conditions and variations of the external environment. In a few cases of interspecific communication that have been discovered, only locative and environmental information seem to be involved, as would in fact be anticipated.

THE AGONISTIC SOCIAL BEHAVIOUR OF *Macaca Mulatta*

By M. R. A. CHANCE

Department of Pharmacology, University of Birmingham

The results of the study on a colony of 253 rhesus monkeys on Monkey Hill at the London Zoo was reported. The main features of the colony were (1) a close affinity and an order of rank between the only three adult males. As reflected in the behaviour of the two top ranking males, the affinity remained unaltered even with the advent of oestrus in a number of females (ultimately ten). (2) The behaviour of the adult females which possessed no constant association contrasted strikingly with that of the adult males.

It is suggested that the bond between the adult males is *per se* an adequate foundation for the sociability of these monkeys, enabling breeding pairs to remain together when sexual conflict is aroused by the simultaneous presence of more than one oestrus female.

The bond between the adult males appeared to have essentially the same structure and to be established in the same way as that between a male and his consort female. Both bonds are a result of an animals response to threat. Two separate components of this response could be

identified, (*a*) an immediate equilibratory response, involving one of a variety of submissive gestures which include (i) adjustment of spatial relations, (ii) submissive gestures (crouching and presenting), (iii) oppositional gestures involving various degrees and types of counter threat, and (iv) an asocial gesture, which consists of crouching or lying bunched up on the ground and has the effect of removing the animal from the social environment; and (*b*) a second response to this threat, occurring much later, is an arousal of interest with resulting attraction towards the aggressor.

Dr. Chance also showed a film of social life in a Macaque colony.

SOCIAL ORGANIZATION IN WILD HOUSE-MOUSE COLONIES

By PETER CROWCROFT

Tolworth

Fighting among laboratory mice is commonly observed, particularly when animals from different families are put together. Most students of this aggressive behaviour have been concerned with the dominance-subordination social systems which arise under certain experimental conditions, rather than with its possible function in nature. Some authors have termed the fighting of mice "non-competitive," but it seems highly probable that it is related to competition for space.

Social hierarchies are formed when small groups of tame male mice are confined together, but when solitary males are allowed to meet by connecting their enclosures, fighting success is seen to be directly related to familiarity with the situations in which the early encounters take place. This suggests that fighting is territorial in function.

When groups of both sexes of wild mice are confined in large pens at certain densities (about 50 mice in 250 sq. ft.), no one male attains dominance over the entire group; small territories are set up and successfully maintained by individual males, which mate with, and tolerate the presence of one or sometimes two females (*in litt.*). The remaining animals frequently investigate the territories but they are always attacked and chased away.

At very low densities wild mice do not form individual territories under similar experimental conditions. It seems probable, therefore, that frequent victory over a number of animals of inferior fighting ability is necessary in order to condition the more aggressive males to expect and obtain victory in particular situations. In a larger space, or a more complex environment than that provided, it is expected that territories would be set up among mice at very low densities.

The females mated with territorial males produce offspring which continue to live within the territory for at least some months after weaning, but females in the "reservoir" groups, subjected to frequent disturbance, may conceive, but do not produce young.

COMPETITION IN WILD RAT COLONIES

By S. A. BARNETT

Glasgow

No précis of this paper is available.

At an Ordinary Meeting of the Association held in the Psychology Department, Birkbeck College, Malet Street, London, on Wednesday, 20th October, 1954, the following papers were read. The President, Dr. A. Walton, was in the Chair.

FINCH COURTSHIP

By R. A. HINDE

Ornithological Field Station, Madingley (Department of Zoology, University of Cambridge)

This paper was concerned with a comparative study of the courtship behaviour of eight species of *Fringillidae*. The methods used were similar to those worked out for other species by Lorenz and Tinbergen. The following were among the topics discussed:—

(i) *Analysis of the tendencies associated with each display posture.* Each posture is associated with conflicting tendencies to attack, flee from and behave sexually to the mate. These can be assessed by examining (*a*) The behaviour shown immediately before or after the posture (cf. Moynihan, *in litt.*), (*b*) The behaviour which accompanies it (e.g. edging towards the mate), (*c*) The components of the posture (e.g. wing-raising, crouching, etc.), and (*d*) The circumstances in which the posture occurs.

(ii) *A Survey of the Changes in Strengths of These Tendencies Through the Season.* In each species the males are dominant in winter. As the reproductive season advances, the tendency to attack the mate decreases and to flee from her increases. This change in the balance between attacking and fleeing tendencies is associated with an increasing tendency to behave sexually (s.s.), and results in a change in dominance. Although a similar change occurs in the female, she lags behind her mate in this respect, and for much of the pre-mating season she is dominant. The precise nature of the dominance reversal varies from species to species: amongst those observed in this study it occurs earliest and is most marked in the Chaffinch.

(iii) *The Nature of the Displays.* In nearly all the species examined the early courtship displays of the males were modified versions of the "head-forward" threat display, which was usually re-orientated so that the male did not face directly towards the female.

(iv) *The Components of the Postures.* For nearly all the components of the displays a relationship can be traced with one or other of the associated tendencies: this remains constant for all the display postures of the species (Cf. Marler, *in litt.*). Thus, raising the wings is associated with attacking, but lowering the primaries with a tendency to behave sexually. Such relationships were found also to be usually constant from species to species . The differences between the postures of the various species thus lie primarily in the ways in which the various components are grouped into displays, and not in the relationships between the components and the associated tendencies.

(v). *Phylogenetic Relationships.* Comparative study of the displays indicates that Canary and Greenfinch are a very closely related pair, to which Goldfinch and Crossbill are also fairly close. Hawfinch and Bullfinch are rather less close to the Greenfinch-Canary stock, and Chaffinch and Brambling are only distantly related to them.

HOW THE HYMENOPTERAN PARASITE *Mormoniella vitripennis* (Walker) FINDS ITS HOST

By ROY L. EDWARDS

Department of Zoology, Hull

M. vitripennis is a chalcid parasite which drills a hole in the puparium of Muscoid flies and lays a number of eggs on the enclosed pupa. It is reasonable to suppose that an olfactory stimulus is important in host-finding, and investigations along those lines have been carried out using a new type of olfactometer (See *Nature*, **171**, 789).

When subjected to the odour of unclean blow-fly puparia *Mormoniella* females pursue a twisting path, but are not attracted directly to the source of the odour. Liver on which blow-fly larvae have fed also elicits this response, but liver which has decomposed by bacterial action does not, nor do puparia which have been cleaned as larvae. The response is therefore not to an intrinsic odour of the puparium, but to the odour of the larval food.

Optical stimulation plays a minor role in

host finding as the parasites only turn aside to investigte a puparium when at a distance of 2-3 mm. from it. They will similarly turn aside to make a preliminary investigation of any small object such as wheat grains, but in all instances the response disappears in a dim red light.

The conclusion to be drawn from the experiments is that *M. vitripennis* finds its host by searching areas which bear the odour of food on which the host larvae have fed, and that this search is undirected until it is within 2-3 mm. of the host.

THE GENETIC AND THE GENETICAL ASPECTS OF BEHAVIOUR

By H. KALMUS

The Galton Laboratory, University College, London

The indiscriminate use, mainly in the American psychological literature, of the words "genetical" and "genetic" causes some confusion and should be avoided. A confusion of terms as well as of concepts seems to be involved. The word "genetic" is the older one and was used by psychologists before the term "genetics" was coined, reputedly by Bateson about 1900, to denote the study of heredity. Thus psychologists have priority when they use "genetic" for the description of situations and faculties (maturation, unfolding, instincts) which arise during the development of a child or young animal. A strict parallel to this is found in descriptive embryology where the ontogenetic phases of development follow each other. Psychogenetic studies are thus primarily descriptive normative investigations.

The adjectives belonging to genetics are "genetical" and less elegantly "genic": consequently, "genetic" should not be used to describe genetical differences. Genetics is in this sense not a normative science and is not concerned primarily with average or representative behaviour but with particular types of variability in behaviour, preferably with segregation in the offspring of controlled matings or among closely related individuals.

As long as the realms of psychology and behaviour study and of genetics were widely separated, the indiscriminate use of the word "genetic" did no great harm, but nowadays one frequently reads papers in which the word "genetic" means ontogenetic in one place and genetical in the next. Unfortunately, in the minds of some students of behaviour there exists some overlap of the two concepts and it is in such cases that the confusion is most dangerous. The behaviourist often contrasts learned and non-learned behaviour, and is apt to call non-learned behaviour "inherited", "genetic", "genetical", "instinctive", "inborn" "innate" or "constitutional." On the other hand, he may call learned behaviour "acquired", "experiential" or some similar term. In this way an accurate, although arbitrary, antithesis is often changed for an inaccurate description, and instead of an analysis of the complex interactions of heredity and environmental factors, some spurious verbal explanation is proferred.

The units of genetics are very remote from "acts" or similar units of behaviour, and simple genetical differences only exert some sort of limiting effect on behaviour. For instance, phenyl-pyruvics are not only deficient in certain bodily symptoms but also show mental defect. Vestigial Drosophila flies have no wings and they cannot fly. It is often said that what is inherited is a capacity for certain behaviour, for instance, for intelligent behaviour, but the definition of capacity is more difficult than some people seem to realise. Some behaviourists overlook environmental factors other than those psychological factors directly concerned with learning—for instance, hormonal or social ones. While these obviously are not experiential, they are, nevertheless, mainly environmental and not genetical.

In general, studies of behaviour will not be greatly assisted by speculation on its genetical components. On the other hand, experimenters may on occasion make use of individual differences which are provided by mutants and individuals which differ in more complex ways from each other.

BOOK REVIEWS

The Emperor Penguin (Apterodytes forsteri) I. Breeding Behaviour and Development. By STONEHOUSE, B. Falkland Islands Dependencies Survey, Scientific Reports No. 6. London: H.M.S.O (1953). 10s. 6d.

The Emperor Penguin is the largest species of the family and breeds further south than any of its relatives. This fascinating study of its breeding biology shows how its behaviour is adapted to the extremely severe conditions at the breeding grounds.

The annual cycle seems to be a compromise between the long growth period necessitated by its size and the short season during which the chicks can be fed intensively. The females desert the rookery after egg-laying, leaving the males to incubate alone, *without food*, for two months. The females return soon after the eggs hatch and the young are later fed by both sexes in crèches. Perhaps the most remarkable feature is the almost complete absence of territorial and aggressive behaviour. This seems to be related to the "huddles" which the incubating birds form when conditions are particularly severe: these serve to conserve body heat and can, of course, only be formed in the absence of aggressiveness.

This paper, illustrated by excellent photographs, is an important contribution to penguin biology and illustrates principles applicable to many other species.

R.A.H.

The Sensations: Their Functions, Processes and Mechanisms. By H. PIÉRON. Translated by M. H. PIRENNE and N. C. ABBOTT. London: Frederick Muller, 1952. Pp. xxiii + 469. 42s.

Perhaps the most fascinating parts of the psychological and physiological territories are those in which the domains run parallel with each other, and the no-mans-land between the two is especially exciting. This is the field covered by Henri Piéron in some 470 highly concentrated pages devoted to the study and analysis of the sensations.

Let no one approach the subject-matter of this book light-heartedly. From the first page onwards the reader is made to think, and to think very hard, but he is led by a master hand along highways and byways through a varied and often uncharted country, and the rewards are many. Perhaps the journey is made more difficult by the fact that the French language is not always capable of being completely translated into English, though the translators have done wonders with a most formidable task and are to be congratulated on presenting to the English-speaking world a work of very considerable interest and importance. The book would have gained by a more free use of simpler English and less use of pseudo-technical terms.

The book is divided into four parts. The first deals, from a more or less evolutionary point of view, with the origin of sensory systems and of the processes by which organisms come to react in specific ways to specific stimuli, and to be able to localise and to measure and assess the characteristics of the various stimuli. Part 2 outlines the physiological mechanisms involved in each of the sense organs. Part 3 discusses the mechanisms by which the stimuli can give rise to the physiological information and nervous activity which is then interpreted as definite sensations, e.g. of colour, tone, fragrance or sweetness, etc. In the fourth part the quantitative aspects of sensation are discussed, and the author analyses how the stimulus is physiologically 'recorded' as to size, spacial distribution, intensity, duration and the various other attributes which it may possess and which may be assessed in a more or less quantitative manner. It may be that this aspect is fundamentally the most difficult part of the whole subject but certainly it occupies nearly half the book and this half is not at all easy to read or assimilate. The treatment of it gains in interest because comparisons are constantly being made between the different sensory mechanisms. For example, a fascinating chapter is devoted to the parts played by sight, touch and hearing in the determination of the spatial aspects of the outside world. However, the constant references first to one sensory mechanism and then to another are likely to cause some embarrassment to the reader, unless he be another Piéron.

The original French edition was produced in 1944. Many alterations have been made for the English translation and the subject has been brought up to 1950. Thus the book cannot be regarded as being the last word and some very important new approaches to the subject naturally receive no mention. Nevertheless, the encyclopaedic knowledge of the earlier literature and the masterly way in which it has

been evaluated should have a sobering influence on the avant-garde among the students of the special senses, and be of immense value to physiologists, psychologists and psychophysicists.

A.N.W.

The Social Insects. By O. W. RICHARDS. London: Macdonald. 1953. Pp. 219. 15s.

Most of the recent books on this subject have been concerned with only one group or one species, but Professor O. W. Richards introduces us to all the kinds of social insects. His book is filled with useful, accurate information. It is well written in good English, so that it is easy to read and understand, and it is decorated with 51 attractive and useful photographs.

The book commences with a good introduction to insects in general, and each succeeding chapter deals with a different group of social insects. Professor Richards' own studies in this field have been in relation to the more primitive kinds of social insects—wasps and humble bees—and he commences his book with, and devotes much attention to, these groups.

The more frequent approach to social insects is via a study of one or other of the socially advanced forms, and this seems to produce a difference in analysis and emphasis. For example, there is the statement (p. 197) that 'The importance of food in the early stages of social evolution may have been much less in insects than it was in man and some of the other social animals.' This conclusion is based only on the absence of co-operation in hunting; it ignores the role of food in the production of a worker caste, and the effect of pre-digested food on brood-rearing and egg-laying. The role of food may have been different, but it was not necessarily less important, in the social insects. Pertinent to this statement is the omission from the bibliography of *The Social World of the Ants* by Auguste Forel (1928), and *The Social Insects* by W. M. Wheeler (1928), the reader being directed only to Wheeler's two earlier books on ants (1913 and 1923). The two omitted books emphasised the importance of food in the social life of ants, and Wheeler attempted to extend his views to cover all social insects. Professor Richards does not discuss this hypothesis at all.

It is stated (p. 169) that 'in reality the differences between the termites and all other social insects are profound and more important than the resemblances.' There may be more differences than resemblances, but the student of social life must consider the resemblances, which will probably be concerned with the necessities of a social system, and he can pay less attention to the differences, which are less likely to be.

Whereas Wheeler's 'Social Insects' was an analysis of the essentials of social life, Richards' book is mainly descriptive of its many facets. As it is primarily designed to interest the general reader, that is no disadvantage.

The biologist who reads it will not quarrel with its facts, and the opinions provoke thought.

C.R.R.

BOOKS RECEIVED

The following books have been received, and in appropriate cases will be reviewed as space permits in early issues:

K. Lorenz (1941)
Comparative Studies on the Behaviour of the Anatinae
Reprinted from the Avicultural Magazine. London: The Avicultural Society. 5s.

Vera Connell (1954)
The Application of Results of Research
London: Butterworth. 21s.

Dennis Chitty (1954)
Control of Rats and Mice. Vol. I & II—Rats.
H. N. Southern (1954)
Control of Rats and Mice. Vol. III—House Mice
Oxford: Clarendon Press. 3 vols. (U.K. only) £5 5s.

Chr. P. Raven (1954)
An Outline of Developmental Physiology. Translated by L. De Ruiter. Pergamon Science Series. London: Pergamon Press Ltd. (U.K. only) 17s. 6d.

Leon F. Whitney & George D. Whitney (1953)
The Distemper Complex
Connecticut: Practical Science Publishing Co., Inc. $5.00.

Angus M. Woodbury (1954)
Principles of General Ecology
New York: The Blakiston Co., Inc. $6.00.

2

ON THE NEURAL BASIS OF THE CONDITIONED RESPONSE*

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A bell sounds and the conditioned dog lifts its forepaw. Although the physiological explanation of this seemingly simple sequence of events has been sought intensively ever since conditioned responses were first discovered more than a half century ago (Pavlov, 1927), we still lack today a satisfactory picture of the underlying neural mechanism. Even the broadest outlines of the neural events remain obscure.

It was first thought that the repeated association of bell and paw movement opened new pathways between the auditory and response centres of the brain. The repeated firing of the two brain centres in association was presumed to leave some kind of residual effect on the interconnecting nerve pathways making it easier for future impulses to travel these same routes. Although now regarded as being much too simple in its original form, this explanation continues to survive with various modifications and qualifications (Konorski, 1948). In particular it is now agreed that the new cerebral associations are more than the direct transcortical linkages earlier supposed, and must involve devious and highly complex pathways.

The physical nature of the residual effects or lasting traces left in the brain remains a matter of pure speculation. Among the wide range of possibilities that continue to receive consideration are the following: growth of new fibre connections, i.e. of axonal and dendritic collaterals and new synaptic endfeet, alteration of transmission resistance at synapses as by expansion and contraction of endfeet or by changes in synaptic membrane permeability, adjustments of excitation threshold within nerve cells or in local portions of their dendritic expansions, specific chemical sensitization of neurons to qualitatively distinct modes of excitation, chemical changes in the neurofibrils and in the neuronal proteins, selective sensitization of neurons to specific spatial patterns of activation, and even structural and chemical changes within the glia.

As an alternative to the notion of the brain traces or engrams as static changes in brain tissue, it has been suggested that the traces might take the form of perseverating eddies of active discharge maintained in self-reexciting circuits (Hilgard & Marquis, 1940; Young, 1938). However, the fact that conditioned responses ordinarily survive deep anesthesia, electro-convulsive shock, epileptic seizures and other disruptions of functional continuity has seemed to rule out any explanation expressed entirely in these dynamic terms.

There remain, nevertheless, certain explaatory advantages in the dynamic form of brain trace, and in a recent advance in learning theory a dual form hypothesis has been proposed (Hebb, 1949), that incorporates the benefits of both the older static and the newer dynamic type of memory trace. In this dual scheme, self-maintained reverberatory excitation is held responsible for the rapid short-term effects in learning and conditioning. In time the continued reverberatory activity is presumed to lead to permanent micro changes in brain morphology that make possible long-term retention of conditioned responses and their survival through states of deep coma, electro-convulsive shock, and the like.

In general the physiological theories have thus far tended to neglect a factor that long has been recognized in psychological studies to be an important element in conditioning namely, the so-called "anticipatory set" or "expectancy."† The incorporation of this factor into the physiological picture leads directly to significant revisions in our thinking about the underlying neural mechanism and to a modified hypothesis which, though somewhat increased in complexity, appears nevertheless to fit better the whole complex of the conditioned response including some of its more paradoxical features.

Following this approach we are lead to postulate as an important aspect of the conditioning process the intermediation of complex high level patterns of central nervous facilitation, i.e. the neural counterparts and derivatives of the psychological expectancies

* From a paper presented in a Symposium on the Physiology of Learning, September 2nd, 1953, at the XIXth International Physiological Congress, Montreal, Canada.

† For a recent discussion of the expectancy factor in conditioning see L. E. Cole (1953) *Human Behavior*, pp. 257-304.

and anticipatory sets. The pattern of central excitation aroused in the brain by the conditioned stimulus can then be assumed to be governed by an intermediate pattern of transient facilitation, rather than being channelled directly by neural engrams or traces as traditionally conceived. Unlike the dynamic traces of earlier theory, the central facilitory pattern or "set" is not a simple vestige or trace of cerebral excitation involved in an earlier pairing of conditioned stimulus and response. It represents rather, a novel and relatively independent organization arising out of high level cerebral activity such as insight, expectancy and the like. In this hypothesis, the permanent structural changes for long-term retention do not help directly to form new associations between sensory and motor centres. Instead they reinforce the intermediary expectancy or facilitory set.

The concept of the central facilitory set and its role in conditioning is best illustrated perhaps with reference to a simple voluntary reaction in man. Let us suppose that electrodes have been taped to the hand of a human subject and that the person has been instructed to lift the hand promptly when a bell sounds, on the penalty of receiving otherwise a severe electric shock. At the sound of the bell, his hand jerks upward instantly, just as quickly as does the paw of the conditioned dog. In the human subject this withdrawal response at the sound of the bell involves a novel pattern of central excitation, which is not the product of any long training, or repeated pairing of bell and shock stimuli. There is no grooving of the fibre pathways between receptor and effector centres of the cortex. In fact, the particular train of central excitation set off by the bell may never have occurred previously in the person's lifetime.

Under these circumstances we say that the human subject gets himself physiologically set to make the proper response at the sound of the bell. The brain pathways for arm flexion become temporarily opened while those for innumerable other possible reactions are temporarily closed. In other words, the prevailing distribution of excitation and inhibition in the brain circuits opens the way for the bell stimulus to release instantly that specific response for which the circuits are adjusted. Once the circuits are properly set, extraneous sensory excitation tends to be absorbed without effect and incompatible reactions are excluded. The novel motor effect of the bell stimulus derives in this case, not from any new pattern of structural pathways but rather, from a new pattern of central excitation and facilitation.

We note that the human subject could just as easily set himself to make the reverse response (i.e. to depress the hand instead of lifting it in which case the excitatory sequence initiated by the bell discharges with equal rapidity into the antagonist muscles. The transient brain set could be patterned likewise for a reaction with the foot, or with the opposite hand. In each case, the specific and immediate motor effect of the incoming auditory impulse is determined by the particular facilitory set that dominates or prevails in the brain at the time the sensory excitations enter.

These governing facilitory sets may be generalized or specific in their organization on both sensory and motor side. For example, a person could set himself to respond only to a bell of low pitch and not to one of high pitch. Or, his set might be quite nonspecific such that any loud noise would set off the reaction; even a sudden tactile stimulus might suffice. Similarly on the motor side, a single response may be rigidly predetermined, or a choice of two responses made possible, or any of a given category.

The main point to be emphasized is that a purely transient, dynamic setting of the brain circuits, in terms of active facilitation and inhibition, is quite capable by itself of causing the bell stimulus to set off a particular limb movement. There is no need here for any new fibre pathways, chemical traces in the neuroplasm, or new synaptic associations. It is evident, furthermore, that *the same response, or other responses, could be coupled functionally in a similar manner to any neutral stimulus* (*of the type employed in conditioning*) *simply by an appropriate adjustment in the cerebral facilitory set.* (In referring to these transient adjustments of the brain mechanism as *facilitory* sets, it should be recognized that the central *inhibitory* phase of the process may be fully as important as the facilitory.)

There is much to suggest that the coupling of bell and forepaw response in the dog during conditioning is achieved through the development of a comparable cerebral facilitory set. The bell-shock expectancy that it takes only a moment to convey to the brain of man with the aid of language, may require hours or days to develop in the brain of the dog by the more roundabout method of example and experience.

Eventually as a result of training, the dog comes to expect the shock at the sound of the bell. More than this the dog comes to anticipate both the bell and shock so that by the time the bell sounds, the dog already is actively prepared in advance (like the human subject) to make the correct forelimb response.

We may thus suppose that in the brain of the conditioned animal a well-organized facilitory set appears prior to the incidence of the conditioned stimulus. It is this special pattern of central facilitation—absent before training and developed through training—that is directly responsible for channelling the sensory impulses into the proper motor response.

The activity of these cerebral facilitory sets is not confined to conditioning and voluntary reaction. They operate continually in behaviour and constitute a prime factor in the control of all brain function. Thinking, perceiving, recognizing, imagining, reasoning, reflex activity, learning, and remembering, as well as conditioning and voluntary activity, have all been found in the laboratory to be profoundly affected by the so-called "mental set" (Gibson, 1951). It is by means of differential facilitory sets that the brain is able to function as many machines in one, setting and resetting itself dozens of times in the course of a day, now for one type of operation, now for another. In short, a great deal of the plasticity in vertebrate behaviour, including that of conditioning, is made possible, not through structural remodelling of the fibre pathways but through dynamic readjustments in the background of central facilitation.

To account for the long-term retention of conditioned responses, one must infer further that the facilitory sets and associated dynamic readjustments become reinforced by some permanent type of neural trace, or engram. In considering the problem of the patterning of the brain engrams, it is all-important that one does not lose sight of the primary role played by the above dynamic factors. Even after a long rest interval, or electrochock treatment, the conditioned response is still dependent upon a preliminary rearousal of the anticipatory set. If the proper pattern of central facilitation has not been established by the time the bell sounds, the conditioned forepaw response fails to occur (Cole, 1953).

A number of implications regarding the nature of the static engram are incorporated in this approach to conditioning, some of which may be stated briefly as follows: (*a*) The engrams for a conditioned response do not take the form merely of new associations between the receptor and effector centres of the brain, however complex. A different type of engram pattern is implied, namely, a pattern so designed as to facilitate, at the proper time and place, the establishment of the correct expectancy and facilitory set. (*b*) With much of the burden of the detailed patterning of the conditioned response relegated to the dynamics of cerebral facilitation, the engrams themselves need be much less extensive and complete than is otherwise necessary. Relatively small changes at critical points may be sufficient to reactivate a given anticipatory set in the proper dynamic background. (*c*) The static engrams on the one hand and the dynamic facilitory patterns on the other are regarded as co-functions, i.e. the operation of the two factors in long-term retention becomes mutually dependent with the conditioned response being a product of the combined action. (*d*) Since the engrams reinforce higher level cerebral activity, they are believed to be complex and diffused rather than localized in nature even in the very simplest conditioned responses. (*e*) The engram patterning is further complicated by the fact that the engrams must function in large part to support the transitions between the expectancies and sets as well as the facilitory patterns per se.

There are definite advantages from the engineering standpoint in having the permanent alterations of the brain designed to reinforce the higher level intermediary facilitation, instead of having them affect the sensory-motor associations directly. This makes it possible, to mention just one advantage, for different (even antagonistic) motor responses to be linked simultaneously to the same sensory stimulus, something that may be desirable to suit different circumstances. This scheme also provides much more readily for that class of phenomena included under the terms "sensory and motor equivalence." In general, with this kind of arrangement, the sensory and response mechanisms of the brain do not become tied down nor selectively modified for specific habits, but remain free to be used in various ways and in various combinations in all categories of behaviour.

This description of the neural events also accounts more readily than earlier theories for findings like those of Lashley (1950) and others on the effects of brain extirpation. Consider the difficulty, on this basis of trying to ablate

even so simple a habit as the conditioned paw movement mentioned above for illustration. One might eliminate the conditioned response by extirpating enough of the auditory centres of the brain to prevent the stimulus from reaching the anticipatory set. However, if the facilitory set is strongly organized, very little stimulus is needed to trigger off the response. In fact, it is known that the response may occur spontaneously under certain conditions without any outside stimulus. Any small remnant of the primary sensory area that would permit the impulses from the bell to filter through to the central facilitory set would be enough to trigger off the conditioned response.

Similarly on the motor side, any undamaged motor mechanisms by which the animal can achieve the desired effect will be sufficient. The ability to switch quickly from one motor pattern to another to accomplish an end (motor equivalence) is already an intrinsic property of the brain. Once the dog learns that contact with the shock electrode must be broken immediately after the bell sounds, any remaining means available is automatically called into play to accomplish this end. Consequently extensive and widely paralyzing lesions in the motor cortex are required to prevent an animal from making a conditioned response in one way or another. For some learning situations any residual ability to move at all may be enough to carry out the learned performance.

To effectively destroy by surgery the engrams themselves or the expectancies, insights, and sets which they reinforce is equally difficult. According to the foregoing, the constellation of engrams for even the simplest conditioned response tends to be complex in design and diffused through the brain, and thus highly resistant to local ablation. Further, the intermediary central facilitation is reinforced from all sides by a great mass of stimuli, associated not only with the conditioning chamber, but also with the situations leading to it, with the experimenter's person, even with the home cage and with various related events in the diurnal cycle. To eliminate by brain damage the channels for all these reminders of the conditioning experience would be prohibitive.

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SOCIAL DOMINANCE RELATIONSHIPS IN A HERD OF DAIRY CATTLE

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Statement of Problem

Most people realize that if two animals are within each other's range of perception, be it visual, olfactory, tactile or other, then the behaviour of each is somewhat modified with respect to the other. Further, when two or more animals of the same species live in close proximity to each other, then there may exist a pattern of group behaviour fully as complex as the behaviour of the individuals comprising the group.

Dairymen have for years recognised the economic importance of the behaviour of their animals. Such phrases as "fidgety cows," "nervous temperament," "milk from contented cows" and the like, bear testimony to this recognition. However, few dairymen have applied deductions drawn from the actions of the individual cows to the behaviour of the herd as a group; indeed, few investigators have recognized the distinction between a group pattern and a group of individual behaviour patterns. The object of this study, therefore, is to describe a type of social organization existing within a herd of dairy cattle, and to explore the effects of this organization on the behaviour of the individuals.

Little has been reported on the social behaviour of ruminants until fairly recently, when Scott and his co-workers began series of experiments on social organization and leadership in sheep and goats (Scott, 1942, 1946). Alverdes (1935) described the behaviour of herds and packs, with particular emphasis on sex and mating behaviour in many species of free-living mammals but made little mention of dominance relationships. More closely concerned with ruminants, Altmann (1952), noted organizational trends in the social behaviour of free living elk. A certain amount of intensive investigation into the organization and behaviour of deer was initiated by Darling (1937), and interest in this group has continued through the years (Darling, 1952).

An understanding of dominance orders in dairy cattle seems to have been taken for granted by Woodbury (1941) when he discussed how the rank or "hook" order of the herd changed upon dehorning the "boss" cow. Actually, the writers can find no direct reference to dominance orders in cattle prior to Woodbury's article. Dove (1936) discusses the relative merits of a one-horned cow over a two-horned cow, but no mention is made of dominance orders as such. Woodbury's conclusions (*loc. cit.*) were that the "hook" order in horned cows was largely determined by the size, shape and effectiveness of the horns; in dehorned cows, the "bunt" order was determined largely by strength and tenacity in pushing, with tenacity being a somewhat loosely defined variable. During the period from 1944 to 1948, Guhl and his co-workers (Guhl *et. al.*, 1948) started a detailed study of "bunt order" in a large dairy herd with emphasis on the physical and physiological factors affecting intra-herd relationships. Unfortunately this work was never completed, nor was any part of it published. Somewhat more recently, Hancock (1950) recognised the importance of taking "herd laws" in consideration when conducting grazing studies. In the same article, he emphasised the point by delineating the dominance order existing in his herd of ten pairs of monozygotic twins. Other than these few reports, the authors know of no intensive, large scale study of herd behaviour from a "dominance order" point of view.

Background Information

To understand the methods used in this study, it is necessary first to have a clear picture of the management routines and herd composition at this station, and second to be generally familiar with manifestations of "normal" individual behaviour patterns. This study was conducted at the Iberia Livestock Experiment Station, Jeanerette, Louisiana, a field station owned and operated by the Dairy Husbandry Research Branch, Agricultural Research Service, U.S. Department of Agriculture.

Management Routines

For convenience of management, the herd is divided into five major groups, each group representing a particular stage in the development or physiological state of the animal. These groups will best be understood by tracing the development of a typical animal from birth through her first lactation period.

Generally, parturition occurs on pasture; within a few hours after birth, the calf and her mother are placed together in an 11 by 12 foot stall. From this stall, the calf can neither see nor smell any other herd animal except her mother. They remain together for three days, during which time the calf receives the benefit of the colostrum, or "first milk."

Three days post-partum the calf is permanently dehorned (electrically) and isolated in a 3 by 5½ foot stall. She spends 30 days in this stall, from which she can hear others and see the heads of young calves in adjoining stalls; it is possible for two adjacent calves to nose each others' head regions.

After 30 days of age, the calf is transferred to a 5 by 11 foot stall which she will generally share with one or two other calves of about the same age. In this, the "two month stall," the calf has a little more space to romp, and can easily observe other calves up to six months of age. In addition, she can nose, sniff or otherwise investigate her stallmate or even calves in adjacent stalls.

At the age of three months, the calf is introduced into what is termed the "young group," a group of 10-15 heifers between three and six months old. The young group pen inside the barn is only about 11 by 35 feet, but it adjoins a one-quarter acre outdoor lot, with free access from inside to outside. Except for being born outdoors, this is the calf's first introduction to green grass and direct sunlight. At six months of age, she is weaned and transferred to the "middle group," which is comprised of 6 to 12 month old heifers. This group is allowed considerably more space both indoors and outdoors and the animals do a limited amount of grazing on their one acre lot. The size of this group varies from 10 to 19 animals.

When the heifer reaches one year of age, she is transferred to the "front group," which spends all of its time on pasture. This group consists of nulliparous heifers over 12 months of age plus a few dry cows which are due for breeding or calving; the average size of this group is about 35 animals, but this figure may vary from 15 to 50 animals. The front group subsists entirely on pasture herbage which is supplemented with grain-feeding during December, January and February. The heifer is bred for the first time during the first heat period observed after she is 18 months old. Breeding is strictly controlled and copulation is brief: the heifer is stanchioned in a breeding chute and after a short period of vaginal sniffing and licking, the bull will generally mount quickly and complete coitus.

About a month pre-partum, the heifer is transferred to the "wet" or milking group, which consists of all the cows in milk. This is by far the largest single group on the farm, and averages about 70 animals. During the major portion of this investigation, the wet group was made up of Jerseys and Sindhi × Jersey halfbreed cows. The young, middle, and front groups were made up of Jersey and crossbred (Jerseys with varying amounts of Red Sindhi blood) cows and heifers.

As mentioned above, parturition occurs out on pasture, and the cow spends the first three days post-partum in isolation with her calf. After the three-day isolation period, the cow is returned to the wet group and milked twice daily (at 4 a.m. and 2 p.m.) for the remainder of her lactation. A daily record of productivity, in terms of pounds of milk, is kept for each cow as long as she is in the herd. It is perhaps pertinent to note at this point that she generally will not see her calf again until the calf in turn is ready to calve more than two years later.

At the first observed heat period three months post-partum, the cow is again bred and, assuming successful conception, is therefore pregnant throughout most of her lactation. Ideally, the cow should bear a calf each year and lactate for 10½ months out of 12. The cow is dried 305 days post-partum.

When the cow is finally dry, she is transferred to the "bayou group," which generally consists of pregnant dry cows more than 30 days pre-partum. When calving time draws near, she is re-introduced to the wet group. Most animals, after bearing the first calf, spend most of their lives with the wet group and only one or two months of the year with the bayou group. As a consequence, the turnover in the bayou group is rapid and the social pattern often does not get a chance to stabilize for any period of time. Group size varies from six to 20 animals, averaging about 15 individuals.

Some cows, however, go dry in less than 305 days (some milk for as few as 100 days) and therefore they spend correspondingly longer periods of time with the bayou group. One cow was used solely for breeding purposes (a damaged udder obviated profitable milking) so that except for about 45 days at calving time, she spent the entire year with the bayou group. Occasionally to facilitate management, the bayou and front groups are combined for several months. At other times, those heifers from the front group which are not due for breeding or calving are put with the bayou group. When this is done, the bayou group contains about 25 to 35 animals, while the front group will consist of about 10-15 animals.

Briefly summarizing, it is important to recognize that the calves used in this study began their social lives (large group conditions) at three months of age; thereafter they were rarely, if ever, by themselves for any appreciable period of time.

Behaviour of the Individual

Before we can attempt to interpret group behaviour patterns, we must have a clear understanding or at least a recognition of the normal individual behaviour patterns. However, since Brownlee (1950, 1954) has already described normal behaviour patterns in cattle, the ensuing discussion will serve to emphasize only those patterns that are pertinent to aggression and social organization.

In cattle, movements that are (subjectively) termed "aggressive" generally follow a definite sequence, each phase of which the author chooses to define as follows: the *approach*, which may be active or passive; the *threat*, or "aggressive intention movement" (Tinbergen, 1952); the *physical contact* (the actual fight) which is followed by victory or defeat.

There is no need to dwell long on the point of *passive approach*, since cattle are extensive wanderers and cross each other's paths any number of times daily. Occasionally, instead of ignoring each other on passing, two cows will engage in a brief manifestation of contesting behaviour. Such contests are usually brief and often go no further than the *threat* stage; however, it is the opinion of the author that these encounters are significant and decisive. (This point will be dealt with more fully during the discussion of "group" behaviour).

Active approach, on the other hand, implies purposeful behaviour and as such requires detailed description and discussion. When a cow is re-introduced to a group after an absence of several weeks or months, she is generally quickly approached and surrounded by many of the group, most of which exhibit investigatory behaviour patterns. A few cows, however, will exhibit "aggressive" behaviour (hard breathing, head lowered, slow deliberate movements, occasional pawing) and move slowly toward the introduced cow. When this aggressive approach occurs, it is fairly safe to predict that *physical contact* will occur between the two animals unless the newcomer flees; the author has termed this action the "active" approach, or "challenge" to distinguish it from the more common and casual "passive" approach. An *active approach* may be made over distances as much as 30 yards, and implies that one animal approaches another for the express purpose of carrying the fight pattern sequence to completion.

The next step of the sequence, the *threat*, can be engaged in only when the contesting animals are within about five feet of each other. In the threat, one of the contestants exhibits aggressive behaviour directed toward the other, i.e., head lowered to about halfway between the normal position and the ground, eyes directed towards the opponent, and the broad forehead on a plane perpendicular to the ground facing the opponent. Despite the fact that all animals at this station are permanently dehorned at birth, all the movements of the threat position would serve to direct the horns towards the opponent, just as if horns were present. The threatened cow has but two alternatives: she may respond by returning the threat in a similar manner (head down, etc.) whereupon direct physical combat ensues; or, more commonly, she will exhibit alarm reactions and retreat. In the alarm reaction, she will lurch out of range of the threatener, with head up, and often will direct all her activities to leaving the immediate vicinity of the aggressive cow. Commonly, a threat is a rather rapid occurrence and is easily overlooked by the casual observer.

Direct physical contact between two animals (aside from accidentally brushing against each other) involves either *butting* or active *fighting*. Frequently, the one action involves or closely follows the other, and thus they are often indistinguishable. However for the purposes of this dissertation, a distinction, perhaps artificial, is made. Butting occurs when one animal uses its forehead to direct a blow at another

animal, without any retaliatory action on the part of the struck animal. The entire episode is usually brief, since the struck animal will manifest every desire to escape from the aggressor. The butt pattern clearly follows the *threat*, since threat-position as described above is mostly concerned with readying the forehead (horns) for the blow.

Whereas butts are non-retaliated blows, fights occur when the struck cow strikes back. A fight sometimes occurs following a passive approach, but more often follows the active approach. In both instances, the fight is preceded by the threat, wherein *both* animals exhibit the threatening, aggressive position of head down, snorting, and slow deliberate movements. They may circle each other in this fashion for as few as five seconds or as much as ten minutes, with their foreheads parallel and less than about four feet apart. At some point in the circling, the fight will suddenly erupt. There will be much shifting of position for a better footing and an attempt by one or both to direct its forehead (horns) for a flank rather than a frontal attack. The animal that can successfully manoeuvre itself around the other so as to be able to hit its opponent in the side is invariably the one that will win the encounter. The flanked animal will make an effort to bring its opponent back to the frontal attack, and if this fails she will flee. When flanking attempts are unsuccessful, the opponents will bring all their weight to bear on each other through the forehead. At this turn of events, the lighter animal is clearly at a disadvantage and steadily loses ground, unless she makes up in agility for what she lacks in weight. Upon flight the defeated animal is chased or followed by the victor for a variable period of time.

A *fight* may consist of but one encounter or more commonly a series of encounters. The actual encounters do not persist for more than about one minute at a time and invariably end with one animal taking flight to regain position. The number of severe encounters will vary directly with the evenness of the match. Two well matched cows may struggle over a period of hours and even days. The interval between encounters may vary from but a few seconds to five minutes. During this interval they will often manifest grazing behaviour patterns despite the fact that the contestants are in a highly excited state; this is accompanied by the customary wandering, but all the while the contestants are both close to and wary of each other. This particular type of diversion agrees well with what Tinbergen (1952) has termed a "displacement activity." Unsuccessful efforts have been made by the writer to try to ascertain whether the between-encounter grazing actually involves the ingestion of grass or is merely a nosing of the ground.

An interesting variation of the fighting pattern occurs when two animals are engaged in rather severe combat. Neither Guhl *et al.* (1948) nor Hancock (1950) make reference to this type of action, and for lack of any other name, the author has termed it the *clinch* manifestation of fight behaviour. In this type of activity, two closely matched contestants have been fighting for some time and one or both show signs of fatigue. They are head to head, and as described above, the more aggressive is manoeuvring for a flanking position. Suddenly, the less aggressive will let her opponent slip its head to her flank but at the same time she will turn her body so that she is standing directly alongside and parallel to the more aggressive animal. In the same "slipping" motion, she will lower her head to a position between the hind leg and the udder of the more aggressive cow, with her forehead on a plane parallel to the ground. As long as she is beside her opponent, the other cow cannot inflict a serious blow since she cannot get into position. The more aggressive animal will make every effort to orient herself perpendicular to her opponent so that she can deliver a telling blow, but she is hampered by the nose in her udder (perhaps interfering with the hind leg movement) and the fact that the less aggressive animal will slide and turn with every effort of the aggressor. The *clinch* seems to be ideal for avoiding damaging blows while pausing for a brief rest, but is not manifested very often since most of the fights are quickly decided.

The younger animals also show manifestations of contest behaviour, but the contests are more of the play-fight type without any decisive outcome (see Brownlee, 1954, for a discussion of play in cattle).

Analysis of Social Rank

Experimental Technique

Observations were routinely made of different groups in the herd (young, middle, front, bayou or wet) in such a manner that each group was observed for at least one hour each week. During the observational period, a note was

made of every contest that could be clearly discerned as such by the observer. The observer was located so that he could see most, if not all of the animals at one time, which usually involved taking a position on top of a truck in the field. Two persons commonly carried out the observations; one continually observed and called out the contests, while the other observed and recorded the contests. On some occasions the recorder could not keep pace with the contests being called out, and thus many contests went unrecorded; on other occasions, the cows were artificially stimulated to induce contesting during periods of lull. For this reason, it is felt that the actual number of contests recorded *per se* is not of much value as an index of herd excitement or even of an animal's aggressiveness. However, this point will be more fully dealt with in a later section.

It is felt that since the animal is normally accustomed to human proximity the presence of the observer had no effect on the eventual outcome of a contest. This was confirmed by occasionally observing some of the groups from such a position whereby the animals exhibited no awareness as to the presence of the observer; the patterns of behaviour observed under these conditions were indistinguishable from those noted when the observer was in full view of the animals. Similarly, the time of day and weather conditions had no radical effect on the observed contesting behaviour. Observations were usually carried out on pasture while the groups were engaged in normal routine activities, although occasionally, a group would be moved to a new pasture to stimulate contesting behaviour.

Herd Order

Allee *et al.* (1949) state that the "contemporary organization of vertebrate groups. . . . is based on the application of three general principles: the holding of territory; domination-subordination; and leadership-followership." Organization as such implies a bond, in that the movements, behaviour or activities of each individual are not completely independent of the others in the group. Thus, we can easily remove a paper clip from a box of clips (an unorganized group) since each unit is independent of the others. However, if the group were "organized" by fastening the clips together, we could not manipulate one clip without affecting some (in a large group) or all (in a small group) of the other clips. The ensuing discussion is based on a "domination-subordination" type of organization within the herd.

The dominance relationship between two cows can be readily ascertained from direct physical contests; to this end, close to 5,000 individual contests within the herd have been recorded by this observer. These were plotted on a large "master chart" on which was entered every animal in the herd. A section of the master chart, showing the details of the marking system, is presented in Fig. 1. Each dot represents an individual contest: by reading across the chart one can determine the victories won by an individual, while reading down would determine her defeats. For example, the chart shows (Fig. 1) that SX34 won three contests

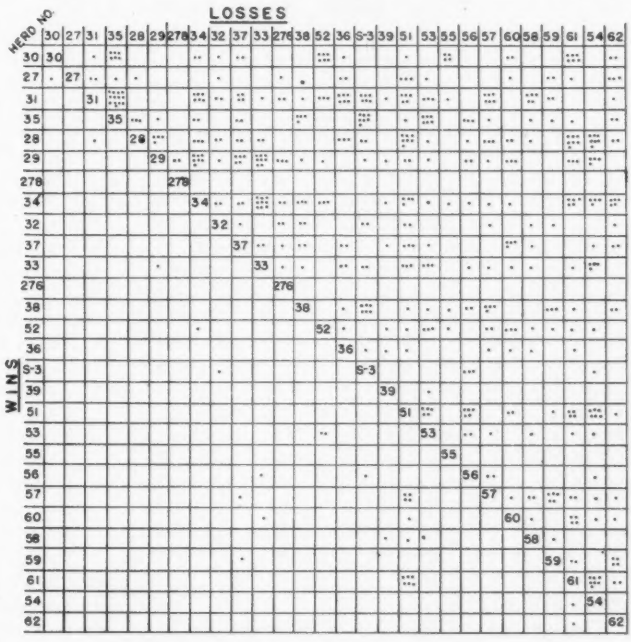


Fig. 1. A representative section of the Master Chart.

over SX38, while she lost two contests with SX35. As more contests were recorded (and therefore more information made available), the order of the animals was rearranged in an effort to get as few dots as possible to the left of the diagonal. In this manner, the animals would automatically be arranged into what is commonly termed a straight-line peck-order, wherein the alpha, or dominant animal of the group, wins contests from all the others and loses to none; the beta animal wins from all the others except the alpha animal; the gamma animal wins from all except the alpha and beta; and so forth down the line until the omega animal is reached, this individual winning no contests and losing to all the others consistently. The terminology is that used by most workers in the field of social organization and was popularized by Allee (1942) in his work on peck order in domestic fowl. Since the particular terms apparently fit the situation in dairy cattle remarkably well, they will be used freely in the ensuing discussion.

The order is demonstrated by the chart (Fig. 1). If no order existed, then it would not be possible to arrange the chart so that more than about 50 per cent. of the dots would lie to one side of the diagonal. However, of the 4,935 contests recorded, only 248, or about 5 per cent. are to the left of the diagonal. A statistical test is not necessary, in this case, to show that this deviation from 50 per cent. is far from being merely a "chance" arrangement.

It was not possible to stage a contest between every pair of animals of the herd; indeed, this would require over 13,000 contests for a herd of 163 animals. In addition, some of the animals died or were otherwise removed from the herd during the course of the experiment. Furthermore, because of the age spread in the herd many of the older animals had never been together in the same group with the very young animals, and so physical contests were not possible. For these reasons it was necessary to assume that if Cow A dominated Cow B, and Cow B dominated Cow C, then Cow A automatically dominated Cow C (if there were no contests recorded between A and C); this assumption was used as a working rule in organizing the chart.

Observational Errors

Every effort was made to keep the amount of error in the observational system down as much as possible, since the errors themselves were difficult, if not impossible to track down and correct. It is pertinent at this time to mention the three main sources of error and the methods of minimizing them.

Perhaps the largest source of error stemmed from a subjective misinterpretation of objective fact. Although the outcome of most of the contests was clearly defined, some few would be considered doubtful. To minimize this type of error, it was necessary to set strict limits on what would be recorded as a victory or defeat in a contest, as follows: if one animal showed an aggressive pattern, with lowered head or just a toss of the head while looking at the second animal, and the second animal reacted to the threat by the characteristic alarm and retreat, then the first was considered the victor in a *threat* contest between the two animals. Had the second animal merely walked away without the lurching alarm and/or retreat, then the contest would have been doubtful and not tabulated. Again, if one animal used its forehead to direct a blow at the second, and the second reacted by alarm and retreat, then the first was considered victorious in a *butt* contest between the two animals. The third and last type of clearly defined contest was the actual physical combat (described above) when one animal finally turned and fled. The rule of retreat was strictly adhered to, and in this manner the degree of subjectivity was minimized.

The next largest source of error was in mistaking the identity of a cow. It is possible by diligent study to distinguish between and "know" each animal of the herd, but even so mistakes are easily made when observing from a distance of 100 feet or more. In an effort to reduce this type of error, practically all observations were made with the aid of a trained assistant who knew the herd well, so that some cross-checking was possible. However, when a group was highly excited and unusually active, one observer was so busy recording what the other called out that he barely had time to look up from his pad; in effect, during periods of intense activity, there was no possible check on the veracity of identity, nor is it possible even to estimate the amount of error introduced.

The third source of error, equally as grave as the above two, was in the recording itself. In the press of trying to record events as quickly as they were happening when 30 or 40 animals were stirring about, it was very easy to write 211 instead of 21 or 311, or the like. During the periods of lesser activity or just after an obser-

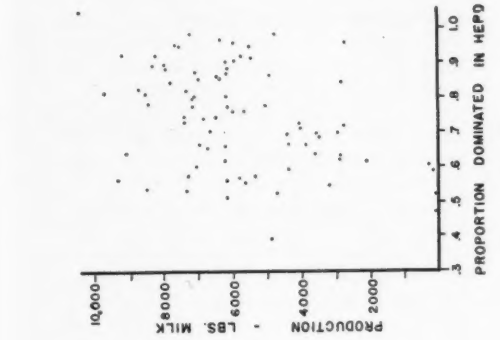


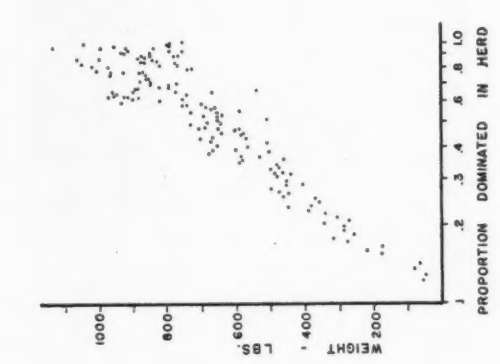
Fig. 2. The relationship between rank order and age.

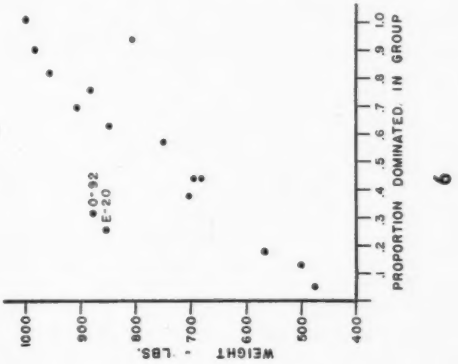
Fig. 3. The relationship between rank order and weight.

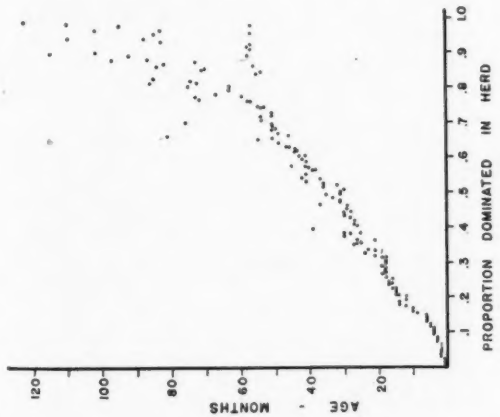
Fig. 4. The relationship between rank order and milk production.

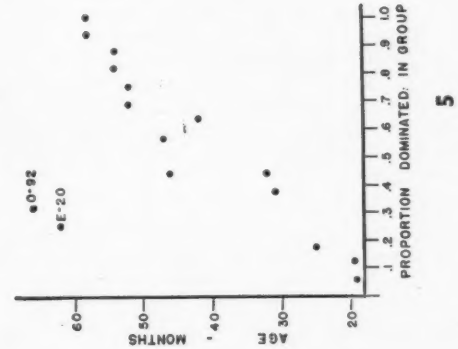
Fig. 5. Shipping group. The relationship between rank order and age.

Fig. 6. Shipping group. The relationship between rank order and weight.









vational period, the observer made an effort to check over the field notes to make sure there were no obvious errors, but still it would be impossible to estimate the amount of error from this source.

Factors Determining Rank

In an effort to get a clearer understanding of the complex of factors which determine an individual's social ranking, the herd order was compared with the ages (Fig. 2), weights (Fig. 3) and first lactation milk production records (Fig. 4) of the animals. (In these and subsequent figures, the "rank order" of an individual refers to the proportion of the herd which she dominates). To calculate correlation coefficients it was necessary to first "normalize" the dominance rank order in the herd; this was accomplished by calculating the area under the normal curve at each rank point and then utilizing a standard table of Cumulative Normal Frequency Distributions (Snedecor, 1945).

Correlation coefficients for rank x age (r_a) find rank x weight (r_w) were highly significant, while that for rank x production (r_p) was of a lower order of significance: $r_a=0.93$, $P<0.01$; $r_w=0.87$, $P<0.01$; $r_p=0.25$, $P<0.05$. On the other hand, there seemed to be little, if any, correlation between social position and the failure to complete the full (305-day) lactation period.

The relationship between age, weight and social rank in this herd can be expressed by the following formula (determined by the method of multiple regression):

$R=0.026\ A + 1.532 \log W - 5.422.$

where R="normalized" social rank, A=age in months, and W=weight in pounds.

It is impossible to determine from these data whether age and weight are causally or coincidentally related to rank. Age is a good index of "seniority" (length of time in the herd), but it does not necessarily include "aggressiveness" which is probably one of the more important factors in the delineation of social rank. By the same token, weight is used as an index of "strength", but it fails to take into account "agility", which may be equally important.

Strange Cow Experiments

Some additional data on the relationship of age and weight to rank order were obtained by introducing two completely strange cows to various groups of cows from this station's herd. The two strange cows (O-92 and E-20) were borrowed from the dairy herd at Louisiana State University; prior to this experiment, these cows had never had any contact with animals out of their "home" herd.

After an initial period of isolation during which they could neither see, hear nor smell any other animals, the two strange cows were introduced first to a group of 14 crossbred culls ("shipping group") and later to a group of two Jersey culls from this station's herd. The introduction of the strange cows to the shipping group was not accompanied by any violent fighting, although there was the usual amount of sniffing and threat activity; after eight days of observation the group's dominance order was determined, and the order was plotted against the ages (Fig. 5) and weights (Fig. 6) of the individuals. An examination of these figures indicates that the two introduced Jerseys are very much "out of line" with respect to age and weight, perhaps more so with age. Three weeks afterward the strange cows were introduced to two Jerseys culls from this station's herd. This time, the introduction was marked by violent and prolonged fighting. Observations made one week later indicated that a rather complex dominance order had been established within the newly formed group, as is shown in Fig. 7.

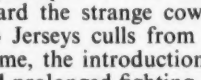


Fig. 7. Dominance relationships between 4 cows. Two cows are from the "home" herd and the other two are "strangers".

The significant lesson learned from this experiment was that the *previously established* dominance relationship between any pair of cows was not disturbed by the presence of the strangers. For example, each of the 14 cull animals in the shipping group was in relatively the same rank position with respect to the others of the "home" herd, despite the introduction of the strange cows. Similarly, J229 had always dominated J245 in the herd, and this relationship continued unchanged (Fig. 7) despite the rather complex order resulting from the introduction of the strange cows. It is interesting to note that O-92 and E-20 ranked fairly low in the shipping group, and yet *all* the animals

in the shipping group ranked below J229 and J245 in the herd dominance order.

These results indicate that although age and weight are closely correlated in this herd, they are not necessarily causally related to rank. Certainly, the data are suggestive that in normal herd management, "seniority" as depicted by age or weight, is highly associated with rank position, and that other physical and behavioural factors may play a major role at the same time.

The Individual as a Member of the Group

Oestrus cycles do not materially affect the established social order, since the rank order has already been described (see above) as a relatively stable type of organization. A cow in heat is usually at a somewhat higher level of general excitement than the others of the group and is usually labelled "nervous." Instead of a normal placidity, she will spend a considerable amount of time approaching and sniffing the others (particularly in the vaginal region) without respect to their position in the social order. It is interesting to note that the sex drive of the individual supersedes organizational characteristics. Whereas under normal conditions the subordinate animal will avoid the dominants under penalty of being butted or otherwise punished, this same animal, when in heat, readily approaches her superiors in the order; even after being repeatedly threatened or chased, she will often continue her efforts to mount the aggressor. Consequently, observations made during the heat period of a cow tend to show considerably more contests involving this cow than is usually the case.

It is pertinent to mention that the maternal drive in a cow immediately post-partum seems to supersede the organizational or herd drive. Immediately post-partum, the mother rests and spends a great deal of time licking the calf, and is apparently oblivious to the rest of the group. When, in the course of normal wanderings, the group moves away, the mother stays behind with her calf and *no longer functions* as a member of the group.

Three days post-partum, the mother and calf are separated. The mother is returned to the wet group, but still manifests *maternal* rather than *organizational* drive patterns although she can no longer see nor hear her calf. She will largely ignore the group, preferring to spend her time near the milking parlour and calf barn; she is restless and bellows continually; she becomes visibly excited at the sight of any of the human handlers. However, two or three days after the separation the maternal drive lessens and the cow returns to the group and normal organizational herd patterns.

The effect of the group on feeding behaviour, particularly grazing, has already been noted by other investigators. Hancock (1950) noted that the cows in a group grazed in unison and that the inclination to ruminate was suppressed if most of the other individuals continued to graze. He also noted that if two groups are separated by as little as a single-wire fence, they maintain separate group grazing patterns; that is, one group may be in the midst of a grazing cycle while the other group would be loafing or lying about.

It would be interesting to try to measure the strength of the grazing drive manifested by the group. Normally, grazing can be easily interrupted by the observer simply by caressing one or more of the pets; others will show curiosity and approach in an investigatory attitude. On other occasions, one cow will stop grazing and wander off toward water, and generally all the others follow, indicating that unless the cow is unusually hungry, the grazing drive is not very strong. It has already been noted above that patterns of behaviour strikingly similar to grazing are manifested between encounters in a particularly violent fight, and it was suggested that the grazing as such might well be a displacement activity. If this labelling is correct, then, according to Tinbergen's hypothesis (1951), grazing would be considered a low threshold activity; this particular point is worthy of a considerable amount of further investigation.

Barn feeding behaviour is also affected by organizational patterns, to the extent that under free group feeding conditions the higher order animals apparently get more to eat. For example, when a group of hungry cows is brought into the barn and offered hay, they will line up at the trough with much shuffling and eat as rapidly as possible. The higher order animals will not hesitate to butt or chase their subordinates away from what apparently looks like a desirable pile of hay, while the very lowest order animals spend a good deal of the feeding time searching for an opening whereby they can get to the hay. Although a quantitative measure of the amount of hay consumed in relation to the order of the animal has not as yet been undertaken, there is little doubt that the lower order animal would suffer markedly if she were

wholly dependant on trough feeding. (Calhoun, 1950, has indicated a direct relationship between the rank order in wild rats and the amount of food consumed). Apparently, "space" is the environmental factor in short supply (thereby stimulating competition) in barn hay feeding, since no spatial competition is evident in open pasture grazing. (For a more complete discussion on minimum environmental factors, see Orgain & Schein, 1953).

It is interesting to speculate as to when and how the order is established in the normal herd routine. The implication from the above discussion is that seniority plays an important role in the rank order. Therefore, barring sickness, injury or an unusual occurrence detrimental to normal calf development, it would seem that the place of each individual in the herd order is determined by the moment of birth. Furthermore, she will advance in the social scale as the older cows are removed from the group, maintaining largely the same relative position with respect to the others in the group.

Normally, intergroup shiftings are accompanied by a considerable amount of excitement and fighting as the introduced animal apparently strives to reassert her place in the overall social scale. The sole exception to this rule is an introduction into the young group, since the three months old heifer has not had any previous contact with the group, and therefore "is not aware of her place." It is interesting to note that the middle group already has a well defined order readily delineated by the observer, whereas numerous observational periods of the young group have yielded little results. In the three to six month old group, *threats* are rare and contests all seem to be of the play-fight type and therefore inconclusive, while in the middle group, *threats* and decisive contests are as common as play-fighting. Until further evidence is available, the hypothesis is proposed that the mechanism of the order is establishd somewhere between the late young and early middle group ages, with perhaps more emphasis on the latter.

Summary

The object of this study has been to describe a type of social organization existing within a herd of dairy cattle, and to explore the effects of this organization on the behaviour of the individuals. Some of the ramifications of the organizational patterns are explored in an effort to trace the development of the organization.

A rather detailed description of the physical plant and management routines at the station where these studies were conducted is presented in the first section of the dissertation, so that the reader who is unfamiliar with dairy herd practices may better understand the ensuing discussion.

Aggressive behaviour patterns of the individual are also described in detail so as to afford the reader a clearer understanding of the role of the individual in the group. Such behaviour apparently follows a definite sequence, each phase of which is discussed in detail. The various links in the chain of aggression are termed: the *approach*, the *threat*, the *physical contact*, and the ensuing victory or defeat. The *approach* may be active or passive; while passive approach merely describes the chance meeting of two cows engaged in random wandering, active approach implies purposeful behaviour on the part of one or both of the animals.

Direct physical contact between two animals involves either butting or actual fighting. Butting is defined as when one animal uses its forehead to direct a blow at another without any retaliatory action on the part of the struck animal. On the other hand, fights occur when the struck cow strikes back. Commonly, a *fight* consists of a series of encounters; the actual encounters do not last for more than about a minute at a time and invariably end with one animal taking flight. The interval between encounters may vary from a few seconds to five minutes, with "displacement grazing" being the major activity between encounters. Actually, most contesting actions observed did not progress further than the *threat* stage, although these contests are considered just as decisive as if they had progressed through the *fight* phase.

Each group in the herd was observed for at least one hour a week during the course of this study. During the observational period, careful notes were kept of each animal involved in a contest, and the outcome of the contest was recorded. Close to 5,000 individual contests were recorded and were plotted on a large master chart. The pattern of wins and losses clearly indicated that the herd was organized in a straight-line peck-order very much like that previously described by workers in the field of domestic fowl.

The dominance order was compared to the ages, weight and production records of the

animals. A highly significant relationship obtained between rank and age and also between rank and weight, but the relationship between rank and milk production was inconclusive. The correlation between rank and the failure to complete a full lactation period was of a low order of significance and therefore not considered further.

In an effort to separate age and weight from seniority, two completely strange cows were introduced into a group of fourteen animals from the experimental herd. After the new group had stabilized, the dominance order was again plotted and it was found that the two introduced cows were very much "out of line" with respect to age and weight. Later, when the two strange cows were introduced to two high ranking animals from the experimental herd, the group of four set up a rather elaborate circular type of dominance order. This particular order did not show any relationship to age or weight, although it was markedly affected by the previously established relationships within the pairs of animals. Hence, it is concluded from these results that although age and weight are closely allied to the social scale pattern in the herd, they are probably not causally related. The data are suggestive that in normal herd management, seniority, as depicted by age or weight, is of primary importance in the determination of rank position. The socal position of each animal is probably determined at three to six months of age, when she first encounters large group living conditions.

Acknowledgments

This work would not have been possible without the assistance and full co-operation of a number of people from entirely different walks of life. The author is particularly indebted to Mr. J. J. Vizinat, Dairy Husbandman, for assistance in many of the field phases of the study, and also to Dr. D. E. Davis, Johns Hopkins University, for overall direction and advice. In addition, the staff of the Iberia Livestock Dairy Station offered many helpful suggestions and criticisms, as did the staff of the Dairy Husbandry Research Branch, Agricultural Research Service, U.S. Department of Agriculture, Beltsville, Maryland.

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THE DEVELOPMENT OF AN APPARATUS TO RECORD THE JAW MOVEMENTS OF CATTLE

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Introduction

The agronomist has for many years studied the effect of grazing animals on the sward, but it is only in recent years that the reverse effect—namely, that of the sward on the grazing habits of the animal—was considered to merit serious study. In several cases, investigations of this type have taken the form of animal behaviour recording.

All the information published on this subject has been based upon time studies carried out by relays of observers. Results obtained in this manner do not give any information about the intensity of grazing, expressed, for example, as "bites per minute," nor do they give a complete picture of cudding activities; it is possible that the number of boli regurgitated and the number of cuds or chews per bolus may be more important measures of this aspect of behaviour. It would be impossible to obtain such detailed information without the aid of an automatic recording apparatus. Progress in this direction has been made by Johnstone-Wallace (1953), who devised a mechanical means of recording the cudding and chewing activities of cattle housed indoors. A description of a more comprehensive apparatus, built by the authors to record the jaw movements of animals, is given below.*

The Development of the Apparatus

The apparatus is designed to record:

(*a*) Time spent in grazing and cudding,

(*b*) The total number of bites over any given period of at least 24 hours,

(*c*) The number of jaw movements associated with grazing or eating,

(*d*) The total number of jaw movements in chewing the cud.

A pen activated by a switch under the cow's jaw, recording each individual jaw movement on a paper roll, will fulfill these requirements, provided that it is possible to descriminate between jaw movements associated with cudding and eating. With a recorder of this type, it is possible to mark clearly forty bites per inch of paper. If bites are recorded at a rate in excess of forty per inch, they are not distinct and are difficult to count. Visual observations show that animals are capable of grazing at a rate of ninety bites per minute. To obtain a clear record, the speed of the paper must be two and a quarter inches per minute. If the recorder is to operate continuously for twenty-four hours, a paper roll eighty yards in length is necessary. As it is not possible to mount such a large recording unit, together with the power pack required to drive it, on the animal, some link has to be established between the grazing animal and a recording station situated at the side of the field. With free grazing cattle, a transmitter, carried by the animal, is activated by the switch under the cow's jaw. The signals are picked up by a receiver attached to the recording units. The use of an indirect link between the switch and the recorder facilitates the use of a more comprehensive recorder enabling detailed examination of the records associated with grazing activities. With tethered animals, the switch under the jaw can be directly connected to the recorder by means of a light insulated wire. The equipment which has been developed consists of:

(*a*) A switch under the cow's jaw.

(*b*) A small transmitter on the cow's back.

(*c*) A receiver at the side of the field.

(*d*) A recording panel.

(*e*) A paper drive movement.

A Description of the Apparatus

(*a*) The Switch

It is possible for the animal to open its mouth to a greater degree when grazing and yet show smaller jaw movements than when cudding. For relatively long periods incorporating several apparent bites, the jaw may not completely close. This is particularly noticeable when the cow is grazing long herbage; the animal opens its mouth wide and, while the tongue is used to roll the herbage into a form suitable for pulling and swallowing, there are several partial closures of the jaw.

*The electrical circuits were developed by D. W. Shirlaw.

It was found that when a simple spring-loaded switch was correctly adjusted for cudding, it remained in the "on" position during grazing, when the mouth remained in a more open position for long periods. A self compensating switch activated during both grazing and cudding was designed and is shown in Figs. 1 and 5.

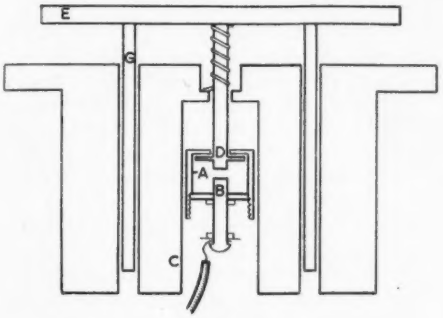

Fig. 1.

This consists of a hollow piston A containing a fixed insulated contact B. The piston is free to move up and down the cylinder C. The position of the piston A in the cylinder is controlled by the movable contact D, which is connected to a plate E. The plate is spring loaded, normally keeping the switch in the off position and the piston A at the top of the cylinder. Downward movement of the jaw plate closes the contacts and any further movement pushes the piston down the cylinder. When the mouth closes, the spring-loaded contact D rises, breaks the switch and lifts the piston A to the top of the cylinder. The top plate is fitted with two guides, G. The switch is made of cast aluminium with stainless steel guides, and brass sleeves and piston. It is enclosed in a metal box for protection, and can be adjusted to work on a change in direction of movement of from 1/32 to 3/8 in. The top plate is covered with sorbo rubber to prevent any possible irritation to the skin.

The switch is incorporated in a standard halter, as illustrated in Fig. 5.

(*b*) The Transmitter

A simple multi-vibrator transmitter was built consisting of two D L 93 valves arranged in a push-pull circuit with a possible maximum output of four watts. The circuit is shown in Fig. 2.

L 1 consists of ten slightly spaced turns, three-quarters of an inch in diameter, of 22 Standard Wire Gauge (S.W.G.) enamelled copper wire and is tuned to 27 megacycles by the 50 picofarad variable condenser C3. Two turns of 22 S.W.G. insulated wire wound into the centre of the main coil constitutes the aerial coupling L 2; this was found to be suitable for an aerial 4 feet 6 inches in length.

The high tension positive passes through a twenty-seven megacycles choke "R.F.C." to a connection at the centre of L 1. The grids of the two valves are connected through two 27 picofarad condensers C 1 and C 2, to this coil. The connections are made on the second turn from both ends. Automatic grid bias is provided by the two condensers C 1 and C 2 and the grid leak resistors R 1 and R 2 each of 10,000 ohms and rated at 0.25 watt; the optimum negative bias was found to be 40 volts. S 1 on the circuit diagram represents the switch under the jaw of the cow; every movement of the jaw closes the high tension circuit and transmits a pulse.

The transmitter and the batteries required to operate it were mounted in metal boxes on either side of a leather saddle (Fig. 6). The R.F. output required to operate the receiver at a range of $\frac{1}{4}$ mile was approximately 2 watts. This was obtained with an anode current of 20 milli-amps at 180 volts, giving an input of 3.6 watts.

(*c*) The Receiver

It was necessary that the receiver should pick up the signals from the transmitter and

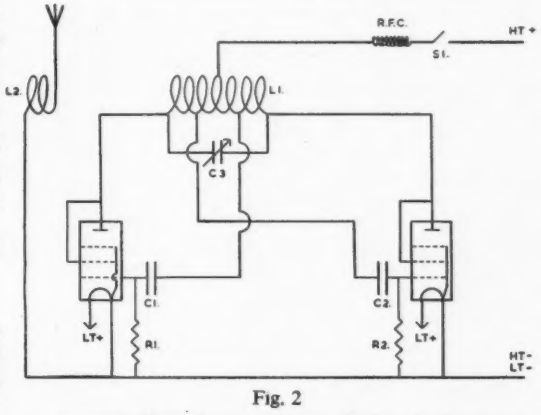

Fig. 2

convert them into a form of electrical energy suitable for operating the recorder. The incom-

ing signal can produce sufficient drop in the anode current of a single valve receiver to operate a sensitive relay which, in turn, will operate the recording panel.

A super regenerative type of receiver, incorporating a single D L. 92 valve, was chosen for the following reasons :

(*a*) It employs the least number of valves.

(*b*) It has high amplification, enabling a weak signal to be used.

(*c*) It has broad tuning and does not lose the sharply tuned signals from the transmitter.

(*d*) It is possible to get a relatively large change in anode current from a weak signal.

The circuit is given in Fig. 3.

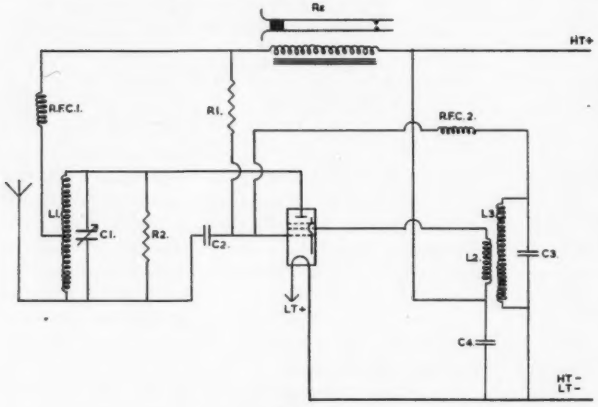

Fig. 3

L 1 consists of six turns of 18 S.W.G. enamelled copper wire, slightly spaced and wound on a three-quarter inch former. It is tuned to 27 megacycles by the 50 picofarad condenser C 1. The high tension positive is connected to a tapping on the coil L 1, two turns from the side connected to the grid, through a radio frequency choke R.F.C. 1. A Siemens relay Type 73, Re, is wired into the lead. Feed back from the anode is obtained by the 27,000 ohm resistor R 1. The 1.5 megohm grid resistor R 2 and the 100 picofarad grid condenser C 2 complete the aerial circuit.

The quench frequency of 50 kilocycles, giving a band width of 100 kilocycles, is obtained from two quench coils L 2 and L 3. L 2 consists of 550 turns of 38 S.W.G. enamelled copper wire pile wound on a former $\frac{1}{8}$" in diameter to a width of $\frac{5}{32}$". The inside lead is connected to the screen grid of the DL 92 and the outside lead to the high tension positive. L 3 is built on the same former as L 2. It has 1550 turns $\frac{1}{4}$" wide, and is separated from L 2 by a thin insulated disc. The inside lead is connected directly to earth and the outside lead through a radio frequency choke, R.F.C. 2, to the control grid of the valve. The 1,000 picofarad condenser C 3 is connected across L 3. C 4 is a decoupling condenser with a value of 0.1 microfarads.

With this circuit the quench of the receiver is such that the valve will not oscillate unless its oscillations are started and continuously boosted by an incoming signal. On breaking into oscillation the anode current drops to five milli-amps from a standing current of seven milli-amps. This drop is sufficient to operate the relay.

The main disadvantage of this type of receiver is its instability, since it is liable to burst into self-oscillation, but this can be controlled by including a 220 ohm resistor in the high tension lead between the radio frequency choke and the coil L 1.

(*d*) The Recording Panel

The circuit diagram is given in Fig. 4.

The power is supplied by a 12 volt accumulator in conjunction with either a mains charger or a petrol generator, each with an output of five amps. The closing of the receiver relay Re 1 activates the 1000 ohm double contact relay Re 2. One set of contacts operates a further 1,000 ohm relay Re 3 capable of carrying the heavy current (750 milli-amps) required to operate the pen recording each individual jaw movement. The second set of contacts activates an adapted ex-R.A.F. Remote Contactor Type 4, R.C. 4. This was modified to give a short contact every ten jaw movements and a longer contact every hundred and twenty. This in turn operates a second pen and also an electromagnetic counter, P.O. Type 400, which records total bites in multiples of ten.

S 1 switches on the power supply which is indicated by the panel light P 1. P 2 shows the closing of the receiver relay. S 2 is a three pole, four-way switch which controls the power to the contacts of the remote contactor and to those of relay Re 3.

The four positions given by this switch are:

1. Off.

2. Completes the circuit to the contacts of the relay Re 3 which operates the pen recording each individual jaw movement.

3. Completes the circuit to the contacts of the remote contactor which operates the P.O. Type 400 counter and the second pen.

4. In this position both circuits are complete.

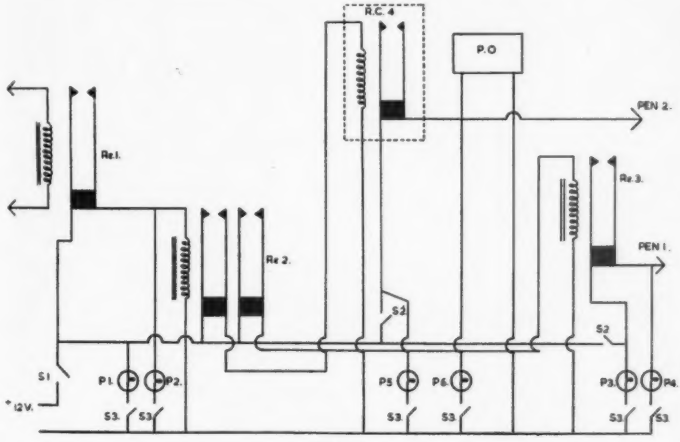

Fig. 4

This switch is included to facilitate the servicing of the recorder by isolating faulty sections of the circuit without interrupting any experiment in progress. Four warning lights are wired into the circuit to locate possible faults. P 3 and P 5 indicate that power is available at the contacts of the relay Re 3, and those of the remote contactor respectively. P 4 and P 6 indicate the closing of these contacts. The power consumption of the recorder was found to be high and to conserve the accumulator a six-pole double contact switch S 3 was included to switch off all the warning lights when not required.

Fig. 7 shows two recording panels each consisting of two recorders. It also shows a clock which has a contact on its "seconds" hand to give a pulse every minute operating a third pen.

(*e*) The Paper Drive Movement and Pen Assembly

The paper roll is driven by a small 12-volt electric motor at a speed of from $\frac{3}{4}$" to 6" per minute. The speed is normally controlled by a rheostat to 2" per minute. Commercial type ball point pens, activated by electro magnets, are used to record the data. Each unit records the activities of two cows, and in Fig. 7 two combined units are illustrated.

Data Recorded by the Apparatus

The type of record obtained is shown in Fig. 8.

The two strips of recording paper illustrate the type of record obtained from two animals when eating cut herbage and when chewing the cud. Each strip of record is marked by five pens, the two outside ones recording each individual jaw movement for the two cows. On the two adjacent pens every ten and every one hundred and twenty bites are marked. The centre line records time intervals of one minute. The difference between the grazing and cudding records is quite distinct, the former being continuous and irregular in nature, the latter being very even but with distinct breaks, each representing the swallowing and regurgitation of a bolus of food.

In using the apparatus it has been found possible to obtain the following information:

(*a*) The number of bites eating per minute.
(*b*) The total number of bites for any one period, and, when the cows are on a controlled diet indoors, the number of bites per pound wet or dry matter consumed.
(*c*) The number of bites cudding per minute or per pound wet or dry matter or per bolus.
(*d*) The number of boli per minute and the number of boli per pound of feed.
(*e*) The time taken for each of these activities.

The data obtained over a 24-hour period from one cow which was fed a weighed amount of silage is given below:

Total numbers of bites (eating)	9,130
Time spent eating	121 minutes
Total number of bites (cudding)	16,630
Total number of boli	393
Time spent cudding	314 minutes
Miscellaneous jaw movements	270
Time spent idling	882 minutes

The apparatus has been used successfully to record the behaviour of cattle housed indoors. Records were taken from four cows consuming

weighed quantities of different types of roughage. The switches under each cow's jaw were connected to the recording panel by overhead wires. The data obtained from these trials will be published on completion of the analysis of the results. The radio link was successfully used on one cow during the summer of 1953, and is now being redesigned for use with four cows.

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PLATE I

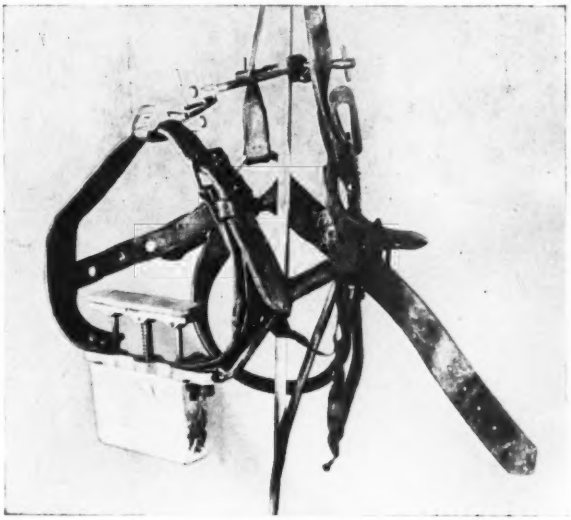

Fig. 5

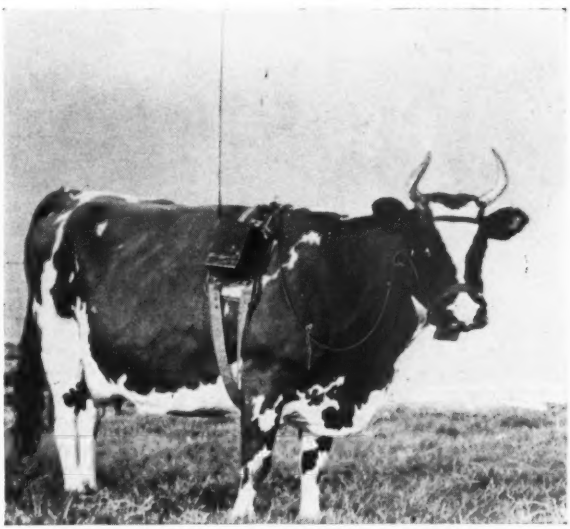

Fig. 6

(*Brit. J. anim. Behav.* **3**, 56-60)

PLATE II

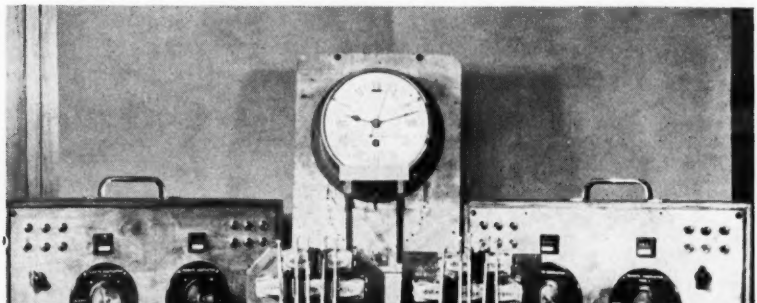

Fig. 7

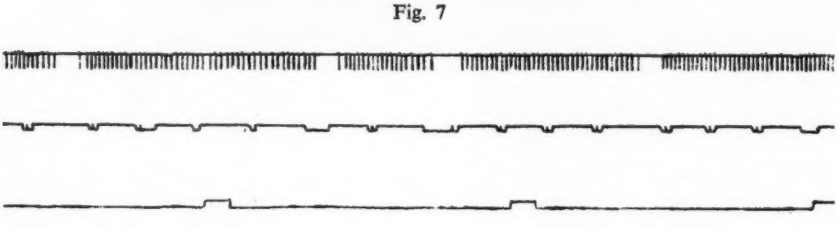

Fig. 8

THE ADAPTABILITY OF BUMBLEBEES TO A CHANGE IN THE LOCATION OF THEIR NEST

By J. B. FREE

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Introduction

Studies of locality learning by honeybees (*Apis mellifera*) have shown that they are capable of quickly adapting themselves to changes in the position of the entrance to their hives, e.g. Bethe (1898), Wolf (1927), Ribbands & Speirs (1953). This is not surprising as the method of colony increase in honeybees by swarming necessitates that the bees in the swarm shall quickly learn the chief features of a new home which may be near to their old one. In the case of *Apis dorsata*, *Apis florea* and *Apis indica* whole colonies will readily abscond (Butler, 1954) so that all the bees of a colony must orientate themselves to their new environment.

The following investigations were carried out in order to study the ability of non-swarming and non-migratory bumblebees to adapt themselves to a change in the position of their nest.

Method

In the first experiment a colony was placed a considerable distance away from its previous position, and well outside its normal foraging range so that the bees of the colony would not be able to return to the old nest site. In the other experiments the position of the new nest site was nearer to the old one.

The observer was screened from the flying bees which normally showed no hesitation when they left or entered their nest. The bumblebee colony itself, housed in a modified Sladen nest box was placed on a wooden platform on the same side of the screen as the observer and about three feet from the ground. A glass tunnel connected the nest box to the front of the screen. Bees were given individual distinctive markings with quick drying paints.

Removal Beyond Original Flight Range

Experiment 1. A colony of *Bombus pratorum* was transported about six miles from its original site. Of 25 bees which left the nest on the following day, only two were not subsequently found in it.

The time that bees spent orientating when they first left their new nest site varied from 9 to 50 seconds, with a mean of 29.9 seconds for the 25 bees. A few of the bees which entered the nest tunnel after a few seconds flight came out again after a short period and continued to orientate themselves. Similar behaviour was observed in the other experiments to be described. On entering a nest tunnel at a new site some bees flew out again for a few seconds, as though to check their position, before they proceeded to their nest. The time spent by the bees in orientating themselves to a new position usually became less on each successive exit. Thus the mean time which the bees spent orientating themselves on their 2nd and 3rd trips in the experiment mentioned above was 12.6 and 2.4 seconds respectively.

Removal to a Site Only Three Inches Away

Experiment 2. In this experiment the nest box, housing a *B. pratorum* colony was moved overnight so that its entrance was only three inches to one side of its original position where an empty nest box was placed.

On their first flight from the new position 10 of the 15 bees spent a mean time of 14.9 seconds in orientation flights. The remaining five presumably noticed no change in their environment when leaving. All 15 bees entered the empty nest box at the old site at the end of their first foraging trip but eventually managed to return to the new one. The five bees which had not orientated themselves took a mean time of 29.8 minutes to return from the old site to the new, compared with a mean time of only 3.8 minutes for the 10 bees that had orientated (degree of significance $P < .01$). It appears probable that they eventually found the new nest site by chance. These five bees also spent significantly longer ($P < .05$) orientating themselves on their second flight from the new site than did the 10 bees that had previously orientated (mean time of 23.4 seconds in the former case compared with 10.6 seconds in the latter). These facts illustrate the value of the orientation flight in relation to location learning. All 15 bees were also observed to visit their old nest site at the end of some of their later foraging expeditions.

Removal to a Site Seven Yards Away

Experiment 3. This experiment was designed to study the adaptability of bees to the new conditions when their colony was moved to a position only a few yards away from the old one, well within the area known to its foraging bees.

A record was made of the bees which foraged from a colony of *B. pratorum* on 27th and 30th June. During the night of 30th June the nest box was transferred to a position behind a screen which was seven yards away from the original nest site, an empty nest box being placed in the old position. The new screen was covered with branches in order to make it appear as different as possible from the original white-washed screen. The bees were released the next morning and their behaviour during the next four days was recorded. The nest box was closed each night and opened again on the following morning when observers were present at both the old and new sites.

On leaving the new site for the first time all the bees made orientation flights and the mean orientation time of nine bees was 25 seconds. However, despite this fact 26 out of 32 bees of the bees which had been previously recorded foraging returned to their old nest site during the experiment. Two bees appeared at the old position soon after they had left the new one; one reached it in a few seconds and the other in about two minutes. The rest of the bees took much longer to arrive at the old nest site after they had left the new position, and many of them carried loads of pollen so that they had evidently been foraging. It was found that 23 of the 26 bees which returned to the old nest position managed ultimately to find their way to the new one.

The bees which returned to the old site of the nest behaved in one of three ways. (*a*) On returning from their first few foraging trips a large number of them entered the entrance tunnel and dummy nest box, where they buzzed excitedly. Most of them flew out again, as though to check their position, only to return within a few seconds. (*b*) Many bees, instead of entering the dummy nest box, hovered in front of its entrance for a few seconds before departing to the new position. (*c*) At the end of later foraging trips an increasing proportion of the bees only flew down to within a few feet of the entrance to the dummy nest box at the old site before proceeding to the new one.

Table I gives the numbers of bees which performed the different behaviour patterns on successive foraging trips during the course of the first day. There was a tendency for each individual to follow, on successive foraging trips, the sequence of behaviour patterns *a*, *b*, *c*, outlined above; 13 of the 23 bees followed all or part of the sequence, eight only entered the dummy nest box, one only hovered at the entrance, and one only flew down towards it.

The time taken by individual bees to return to their new nest site after their first arrival at the old one varied enormously—from a few seconds to 219 minutes (mean 43.1 minutes). Since the screens at the two sites were quite different in appearance, it was unlikely that the "lost" foragers found the new site by analogy with the old one. Those bees which took a long time to return had probably occupied themselves by searching for the new site. Foragers which inspected the old nest site without entering the dummy nest box, and then immediately flew to the new nest site had obviously remembered the new position of their colony.

Many of the foragers visited the old site on the second and third days, but none on the fourth day (table II). The 23 bees which were

Table I. Behaviour of Bees in Experiment 3, which visited the Old and New Nest Sites on the First Day.

Trip No.	1	2	3	4	5	6	7	8	9	10	11
No. of bees foraging	23	20	18	16	12	10	9	7	4	3	2
Entered dummy nest box	18	5	2	—	—	—	—	—	—	—	—
Hovered at entrance to dummy nest box	—	4	3	3	3	2	—	—	—	—	—
Flew down towards entrance of dummy nest box	—	2	1	2	6	—	4	2	1	1	1

Table II. Behaviour of Bees which Visited the Old and New Nest Sites during Experiment 3

	1st day			2nd day			3rd day			4th day		
	A	B	C	A	B	C	A	B	C	A	B	C
No. of visits	25	15	20	6	3	18	1	1	7	—	—	—
No. of bees involved	19	11	13	3	3	9	1	1	6	—	—	—
Total no. of bees visiting old nest location		23			13			8			0	
Total no. foraging		23			20			14			15	

A=entered dummy nest box. B=hovered at entrance. C=flew down to within a few feet of the entrance.

recorded at both sites visited the old site for a mean of 4.2 trips. Often they suddenly reappeared at the old site after they had returned directly to the new site for several trips in succession. Their memory of the characteristics of the new site frequently appeared to become less well defined during the period they spent in the nest at night with the result that eight bees visited the old site again after their first trip on the third day, even though they had apparently learnt the new location of their nest perfectly on the previous day. Many of the bees also made orientation flights around the entrance at the beginning of their first trips on the second and third days.

Experiment 4. This experiment was similar to experiment 3 and similar results were obtained. All 11 previously recorded foragers visited the old nest site during the experiment, and eight of them eventually found the new one.

Experiment 5. It appeared possible that in experiments 3 and 4 the bees which visited the old nest site on more than one occasion were using it as a landmark to guide them back to the new position of their colony, although only two of the bees were observed to visit the old nest site *before* they went foraging. In order to investigate this possibility it was decided to place a colony on a site the characteristics of which its foragers had already learnt, so that on their return from foraging they would have no need to orientate themselves to it from their previous nest site.

A colony of *B. pratorum* was moved to a site (position 2) seven yards away from the old one (position 1). During the first two days of the experiment 14 out of 19 of the previously recorded foragers of the colony visited position 1. The entrance to the nest box which housed the colony was closed after dark on the second day, and it was opened again the next morning when the nest box had been replaced in position 1. Twelve of the 14 previously recorded foragers which had visited the old nest site at position 1 during the first two days of the experiment were also foraging on the third and fourth days. Despite the fact that the colony had been in position 1 for a month before the experiment started, so that this location was well known to the foragers of the colony, nine of these 12 bees returned to position 2 at the end of their trips on these two days.

From the results of this experiment it appeared that most of the bees were not using the old nest site as a landmark to the new site. It appeared therefore, that when the old and new nest sites were so close together, returning foragers recognised features of the environment which they had used as orientation marks to the old nest site and then went to it—even although some of them had gone correctly to the new site at the end of the previous foraging trips.

To test this hypothesis a colony was moved to a greater distance from its previous site, so that there was little likelihood that the bees which were returning to the new position of their nest would be "reminded" of the features of the previous nest site.

Removal to a Site Eighty Yards Away

Experiment 6. A colony of *B. pratorum* was moved to a site about 80 yards away from the old one, the vegetation between the two sites being very varied. The mean orientation time of 15 of these bees, on their first trip, was 39.9 seconds. Despite this 16 of the 17 bees previously recorded foraging from the old position entered the dummy nest box on their first foraging trip. Twelve of these bees eventually returned to the new nest site from the old one, although some took several hours to do so. (Mean time 127 minutes +). (One bee was accidentally killed

at the old nest site). "Lost" foragers frequently remained away from the old site for long periods, probably searching for the new position. On later foraging expeditions only one of the 12 foragers went back to the old nest site (on its third trip) on the first day, and none on the second.

It was concluded that once foragers had returned successfully to the new position of their nest they continued to do so on later foraging expeditions—provided that they were not "reminded" of the old nest locality. The long periods of time which many of the foragers spend searching for their new nest site may possibly have contributed toward this result.

Behaviour of Queens and Males on First Leaving Their Nests

A colony of *Bombus locurum* was moved to a new location 4½ miles from its original site. The mean orientation time at the beginning of the first flights of 30 worker bees and 16 young queens was 25.0 seconds and 23.4 seconds respectively. These observations support those of Plath (1934) in indicating that location learning by queens is similar to that of workers. Males were never seen to make orientation flights, although during the course of this and other work several dozen *Bombus agrorum*, *B. lucorum*, *B. pratorum* and *Bombus sylvarum* males were observed to leave their nests on what were almost certainly their first flights. No males of these species were ever seen to return to their own nests.

Discussion and Conclusions

Bethe (1898) rotated a hive of honeybees through 90° and found that homing bees first landed at the old entrance site but that after a short time they returned directly to the entrance in its new position. In a similar experiment Wolf (1927) found that normal rate of incoming of the bees was resumed a few minutes after rotation of the hive. The experiments of Ribbands and Speirs (1953) differed from those of Bethe and Wolf in that the bees were not allowed to fly until after the entrance had been changed; these observers found that after a few trips the majority of the bees returned directly to the new entrance.

The results obtained in the experiments on bumblebees in which the old and new nest sites were only seven yards apart were similar to those obtained in the above experiments with honeybees, although bumblebees were not found to release scent at the entrances to their nests and could not therefore facilitate reorientation of their fellows in the way that honeybees can under similar conditions (Ribbands & Speirs, 1953). Most of the bumblebees (89 per cent.) that had foraged from the nest in its old position returned to it in its new one, although 80 per cent. of these also visited the old position at least once.

In these experiments great variability in learning ability was exhibited by different individuals. Eleven of 62 previously recorded foragers learnt the new site without visiting the old, whilst seven seen at the old site never managed to find the new one. Those bees which were observed at both the old and the new sites showed great individual variation in the number of visits they made to the old site before they learned always to return directly to the new one.

When the new site was 80 yards from the old one, the majority of the bees having visited the old nest site on their first trip, always thereafter returned correctly to the new nest site. It was considered that under these conditions foragers which were returning to the new nest site were not confused by the sight of the old nest location in the way that they may have been in some of the other experiments described.

When a colony in a nest box was placed a considerable distance away from its old position and well outside the normal foraging area 92 per cent. of its foragers managed to return to the new position.

Bumblebees thus exhibit a well marked ability to adapt themselves to environmental changes that are much more severe than any which they are likely to meet in nature. This they accomplished by the adaptation of orientation mechanisms which they require under more normal circumstances, i.e.

1. The orientation mechanism of a bee on its first flight.

2. The searching behaviour of a returning forager, and the re-orientation tendency of an outgoing forager which must be necessary when disturbance has occurred to the vegetation in the immediate vicinity of the nest entrance.

Summary

1. Most of the foragers of a bumblebee colony returned successfully to their nest when it was moved to a new position outside their foraging range from the old nest site.

2. When the new site was within the foraging range of the old a high proportion of foragers

returned to it but most of them, at the end of their first foraging trip, returned to the old site before they proceeded to the new.

3. When the old and new nest sites were close together many foragers also visited the old site at the end of subsequent trips.

4. When the old and new nest sites were sufficiently far apart for the foragers not to be "reminded" of the features of the old site on their return to the new, the majority of them subsequently returned direct to the new site without first visiting the old.

5. Individuals varied greatly in their learning ability.

Acknowledgments

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OBSERVATIONS ON HONEYBEES ATTENDING THEIR QUEEN

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Introduction

The bees in the honeybee colony perform a sequence of duties determined largely by their age (Rösch, 1925). Rösch stated that bees of from one to 28 days old were seen in the circle around their queen, but according to Taranov and Ivanova (1946) only the nurse bees attended her. Perepelova (1928) watched 35 workers of from six to 13 days old feed the queen, but she did not record the ages of any other attendants.

The food of the queen is important in relation to egg-production, and it has been assumed that she is fed on the secretion of the pharyngeal glands of the nurse bees. These glands are only active in the earlier part of the worker's life (when the brood is fed), and so the age of bees feeding the queen is of particular interest. For this reason it was decided to make further observations on this subject and to include recordings of the ages of bees engaged on other duties in relation to the queen.

Method

The observations were carried out on a small but otherwise normal colony consisting initially of about 4,500 bees (visual estimation—see Jeffree, 1951) and a year-old queen. It was housed in a three-frame observation hive which allowed the bees free flight. A distinctively marked group of 100-110 newly-emerged bees was introduced every fourth day from 17th May to 18th June, 1954, thus giving nine separate age-groups. Observations were begun on 18th May and continued until 7th July, when the colony swarmed.

The queen receives food through her proboscis, which is placed between the mandibles of the worker concerned. In the few cases where the queen withdrew her proboscis in less than five seconds no record was made, as doubt exists whether she actually receives food in so short a period (Taranov & Ivanova, 1946).

Preliminary Observations

Sixteen one-hour periods between 26th May and 28th June were set aside for recording the number of eggs laid and the time spent in receiving food from attendants (both marked and unmarked).

In the period 26th May to 8th June the mean number of feeds was 4.8 per hour, and the mean duration of each feed was 37 seconds. In this period the mean egg-laying rate was 22 eggs per hour. In an "average" twenty-four hours between 26th May and 10th June, therefore, 528 eggs might have been produced for a total of 71 minutes feeding by 115 bees. From 9th June the colony was affected by swarm preparations and

Table I. Food Supply and Egg-Production of Queen

	Period I					Period II						
	May 26	May 27	May 28	May 31	June 8	June 11	June 16	June 17	June 21	June 22	June 23	June 28
Observation time (hrs.)	2	2	2	1	1	1	1	1	1	1	1	1
Mean no. eggs per hour	17	17	22	37	18	16	16	27	22	12	27	16
Mean no. feeds per hour	7·0	6·0	3·5	4·0	3·5	3·0	0	2·0	0	0	0	0
Mean duration of each feed (secs.)	34 ±2·9	30 ±6·8	41 ±7·4	41 ±21·1	54 ±24.9	62 ±15·0	—	63 ±42·0	—	—	—	—
Mean no. eggs per hour	22±3·8					19±2·3						
Mean no. feeds per hour	4·8±0·7					0·7±0·5						
Mean duration of each feed (secs.)	37±3·7					63±15·6						

although the number of eggs laid by the queen diminished in the days immediately preceding the issue of the swarm, she did not cease laying. This reduction could be attributed at least partly to lack of suitable empty cells. The mean egg production over the whole period (26th May to 28th June) was 21 ± 2.0 eggs per hour, there being no significant decrease before 28th June (Table I), despite a reduced food supply from attendants latterly.

Frequently, but not always, only one worker supplied food to the queen between each period of egg-laying, as Istomina-Tzvetkova (1953) has stated. Two bees in succession were seen to feed the queen on fifteen occasions (total time ranged from 43 seconds to 161 seconds), and three bees on two occasions (68 to 125 seconds), while there were single observations of four bees (144 seconds) and five bees (140 seconds) supplying food successively.

The number of eggs laid without interruption for feeding was found to vary considerably, being as high as 26 or as low as two. The mean value for five days between 27th May and 8th June was 7.6 ± 1.9 eggs.

Observations on the Ages of Bees Attending the Queen

Usually about eight to ten bees attended the queen. If she was stationary there tended to be rather more, but if she walked rapidly there were fewer with her since some lost contact and others did not quickly replace them. Many bees seemed unaware of the queen as she passed.

Most of the attendants busily examine the queen with their antennae, a few lick her body, particularly the abdomen, while an occasional individual provides food.

On each of 15 days (between 9th and 29th June) the age-groups of attendant marked bees were observed and from four to nine different groups were recorded on any one day. The ages over the whole period ranged from a few hours to 36 days.

Fifty marked bees, of from one to 30 days old, were seen to lick the queen, implying that, as might be expected, any of the attendants could perform this duty, irrespective of age. In 65 observations, only bees less than twelve days old were observed to feed the queen (Table II). so it is likely that older bees do not usually do this.

From these 65 observations, together with 35 more from unmarked bees, the mean time for each feed was 47 ± 2.6 seconds, and individual feeds varied between five and 156 seconds. The feeding time was not affected by the age of worker (Table II). Furthermore, there was no evidence of any change in the duration of feeds during the experiment (see Fig. 1).

For a consideration of the relative frequency with which different age-groups fed the queen, records for dates earlier than 27th May were

Table II. Age of Bees Feeding the Queen

Date of Marking	*Colour Group*	Age (days)											
		0	1	2	3	4	5	6	7	8	9	10	11
17.5.54	Red		1	1	1							1	1
21.5.54	Pink				2							2	
25.5.54	Turquoise			4	1			3		1	3		
29.5.54	Yellow			2	2	1	2				1	4	1
2.6.54	Green						2	2	5				
6.6.54	White				6								
10.6.54	Silver		4	5		2		1					
14.6.54	Gold		1	1									
18.6.54	Blue		1		1								
	Total	0	7	13	13	3	4	6	5	1	4	7	2
Mean duration of each feed (secs.)		—	49	48	42	72	88	28	30	50	75	60	57

omitted, since before then all the marked bees were very young. The time during which the bees were under observation each day varied, and any bias caused by this was corrected by working with the number of marked bees recorded per hour of observation. Results for the period 27th May to 9th June are shown in Fig. 2. In this period the distribution of ages is fairly constant.

Fig. 1. Duration of each feed (daily means). Days with only one observation are omitted.

The first of a fairly rapid succession of queen cups (ignoring one which was formed on 28th May but underwent no further development) was built on 9th June. From this time onwards there was a marked decrease in the number of times the queen was given food (Table I), and young bees now predominated among those which fed her (Fig. 3). Statistical analysis of the difference between the ages of the bees in the two periods, before and after 9th June, gave $t_{(59)} = 5.00$, which is highly significant.

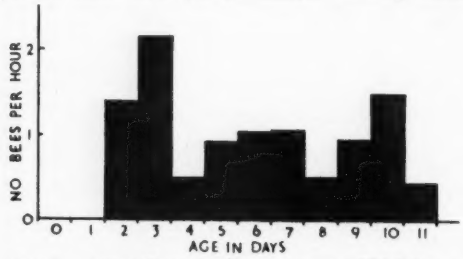

Fig. 2. Ages of bees feeding the queen, 27th May—9th June.

Discussion

The results presented here extend those of Perepelova (1928), very young bees now also being seen to feed the queen. Perepelova, however, does not state when her observations were made, and at a different time of the year the young bees might possibly not take a part in supplying food. The age at which bees feed their queen is probably influenced by the state of the colony, since none older than six days were recorded after 9th June when the main series of queen cups was started.

Perepelova's data show that the mean duration of each feed was 144 seconds, as compared with 47 seconds found here. The difference might possibly be associated with the very restricted egg-production of the queen now studied, due to the limitations of space in the observation hive.

The age-range of bees feeding the queen and of those feeding the larvae are similar (Rösch, 1925; Lindauer, 1952), and this would accord with the view that the queen is fed on the same food as the larvae.

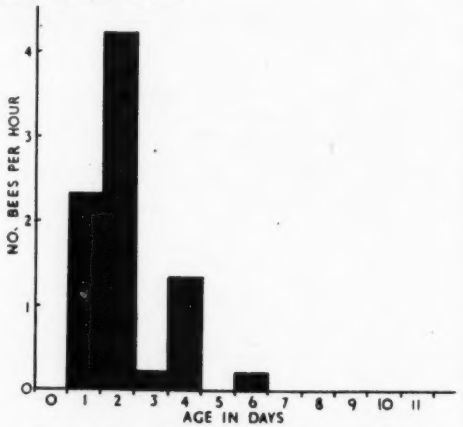

Fig. 3. Ages of bees feeding the queen, 10th—21st June.

Bees well above the age for feeding the queen were found in the circle of attendants, constantly

examining her body with their antennae or licking it. However, no undue excitement was caused by the passage of the queen through a group of bees not recently in contact with her and many made no attempt to follow her, thus giving the impression that there was hardly any competition to tend her.

Summary

1. The ages of the attendants of a honeybee queen, and the time spent feeding her, were observed. The colony was in a three-frame observation hive, which resulted in the rate of egg-laying of the queen being restricted (mean 504 eggs per day). At first the mean number of feeds was 4.8 per hour, but after swarm preparations had commenced the number of feeds declined.

2. Usually only one or two bees (maximum five) supplied the queen with food between each period of egg-laying. The egg-production between successive feeds was observed.

3. The ages of the bees which examined the queen with their antennae varied between a few hours and 36 days. A smaller number of bees, from one to 30 days old, licked the queen. Bees from one to 11 days old fed the queen.

4. The mean age of bees feeding the queen was significantly reduced after the construction of queen cells had started.

5. The duration of each feed was 47 $\pm$ 2.6 seconds. There was no obvious relationship between the age of the workers and the duration of feeds.

Acknowledgment

I wish to thank Mr. E. P. Jeffree for his help and advice during the course of this work.

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A NOTE ON FEMALE STRIDULATION IN THE BRITISH ACRIDINAE (*Orthoptera, Acrididae*).

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Although stridulation in grasshoppers of the subfamily Acridinae is usually observed only in the male sex, it is now well-known that females occasionally stridulate (see especially Faber, 1953 ; Jacobs, 1953, pp. 24 *et seq.*; Ragge 1955) and the regularity with which this sometimes occurs suggests that it forms an important part of their behaviour.

In a recent note the writer (*op. cit.*) described occurrences of female stridulation in *Chorthippus brunneus* (Thunberg), *Myrmeleotettix maculatus* (Thunberg), and *Gomphocerus rufus* (L.); in all these cases the sound produced was as loud or almost as loud as in the males, and was of the same type (sometimes the male and female songs were indistinguishable). Instances of silent stridulatory movements in these species and in *Ch. albomarginatus* (Degeer) were also described. "Soundless stridulations" of this type have also been observed in *Ch. brunneus* by Frazer (1952).

More recently, female stridulation has been observed in two further British species, *Omocestus ventralis* (Zetterstedt) and *Ch. parallelus* (Zetterstedt). In the case of *O. ventralis*, four females were bred in the absence of males and all four stridulated almost every day for over a month. The sound produced was usually typical of the normal song of an isolated male, but it is of particular interest that on one occasion a female stridulated several times in the manner of the male's courtship song. The stridulation of one female frequently stimulated stridulation from one or more of the other females; this occurred so regularly that there can be no doubt that a genuine response was involved. In the case of *Ch. parallelus*, females were frequently observed making stridulatory movements in a cage from which most of the males had been removed. In no case was audible sound produced, presumably because the females of this species have reduced fore wings.

From these observations it is only possible to make very tentative inferences. It seems clear, however, that female stridulation forms a regular part of the behaviour of some of the species mentioned. As suggested earlier (Ragge, *op. cit.*) it is probable that the females only stridulate during a certain phase of their sexual cycle, the infrequent observations of it suggesting that this phase is normally short-lived. As female stridulation seems to be much more prevalent in the absence of males, it is likely that the presence of the latter is responsible for inhibition of stridulation, which would be effected almost certainly by copulation. The conclusion which is suggested by these observations, then, is that female stridulation occurs when the female is in a suitable state for copulation, and that it terminates, at least temporarily, when the latter takes place. In the case of *Ch. parallelus*, the commencement of female stridulation after the removal of most of the males from the cage suggests that the physiological state relating to its occurrence may reappear in the absence of repeated copulation.

On the basis of this hypothesis it is not surprising that female stridulation has been rarely observed in the past, as conditions both in the field and in captivity are usually such that males and females intermingle freely. Physiologically, it is probably of importance that the females are only receptive to attempts at copulation by the male when fertilization is required, and their stridulation may in some cases be a by-product of this receptive phase. The rudimentary nature of the female stridulatory pegs and the poor development or lack of expanded areas in the female fore wings suggest that female sound-production does not in itself form a very important part of Acridine behaviour. The behaviour associated with this stridulation, however, is doubtless of great significance, and a comprehensive study of its physiological aspects is at present being made by Mr. P. T. Haskell of the Imperial College of Science and Technology.

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EARLY RECOGNITION OF THE MANIPULATIVE DRIVE IN MONKEYS

By WAYNE DENNIS
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In a recent series of articles Harlow and various collaborators (Moss & Harlow, 1947; Davis, Settlage & Harlow, 1950; Harlow, 1950; Harlow, & Meyer, 1950) have presented evidence that monkeys can learn to operate some mechanical contrivances, and will continue to operate them for some time, without external reward. These studies show that a manipulative or investigating drive is sufficient to produce learning and to maintain performance. It is a matter of first importance that the existence of activities which have intrinsic motivation be recognised. The lack of a general recognition of such behaviour may be due to the fact that laboratory studies of animals, including researches with monkeys and other infra-human primates, have traditionally supplied extrinsic rewards, and hence the conditions for observing learning and performance based on intrinsic motivation have seldom been present. Had external rewards not been traditional, doubtless the phenomena observed by Harlow and his associates would be better-known to present-day investigators of animal behaviour.

But some of the early observers, perhaps because their perception was relatively unaffected by learning theory, did note the intrinsically motivated behaviour of monkeys. Both Romanes (1882) and Thorndike (1901) gave accounts of specific instances and formulated general statements. No subsequent investigators, however, seem to have been familiar with these observations and principles. Because of the interest aroused by the Wisconsin group, it now seems likely that considerable research will be done on intrinsic motivation in the near future. For this reason it seems appropriate to call attention to what are probably the earliest recorded descriptions of behaviour in monkeys based on intrinsic rewards.

The first set of these was recorded by Romanes (1882). Romanes' observations concern a South American brown capuchin (*Cebus fatuellus*) which he borrowed temporarily from the Zoological Society of London and kept in a private home from December 18th, 1880, to the end of February, 1881. The home was that of Romanes' mother and sister.

His diary of observations refers to many kinds of behaviour. I shall abstract here only the instances of learning and performances not extrinsically rewarded. They are as follows:

1. The monkey learned to push a heavy washstand to which his chain was attached in order to extend his range of movement. Food, with which he was plentifully supplied, did not provide a sufficient inducement to cause him to move the washstand; he did it only when "bent on mischief" such as stripping the leather cover off a trunk which was just beyond normal reach.

2. Because the washstand fastening was unsatisfactory, a ring was sunk in the floor and the chain was now attached to this. "The moment the chain was fastened he began to investigate its new connection, and continued to do so for hours, passing the chain rapidly backward and forwards through the ring. When he found this did not loosen it, he began to hammer it and the ring also with all of his strength, and this he continued to do for the rest of the day."

3. Having obtained possession of the hearth brush, the monkey learned how to unscrew the handle. With great perseverance, he also learned how to replace the handle. "As soon as he had accomplished his wish, he unscrewed it again, and then screwed it in again the second time rather more easily than the first, and so on many times. When he had become by practice tolerably perfect in screwing and unscrewing, he gave it up and took some other amusement. The desire to accomplish a chosen task seems a sufficient inducement to lead him to take any amount of trouble."

4. On one occasion a break in his chain enabled him to reach the trunk where the nuts on which he was fed were kept. Although he had nuts available within easy reach outside the trunk, he worked for two full hours at trying to open the lock of the trunk. Because the lock was a difficult one he did not succeed.

5. He rolled a piece of paper into the shape of a stick, put one end into the hearth until it caught fire, then pulled it out and watched it burn. "I gave him a whole newspaper, and he tore it to pieces, rolled up each piece as I have

described, to make it long enough to reach the fire, and so burnt it all piece by piece."

Romanes concludes "I should say that much the most striking feature in the psychology of this animal, and the one which is least like anything met with in other animals, was the tireless spirit of investigation . . . . I confess I should not have believed what I saw unless I had repeatedly seen it with my own eyes."

Thorndike, who worked with three Cebus monkeys in 1900 and 1901, records one instance of learning without a food reward. He says "No. 1 happened to hit a projecting wire so as to make it vibrate. He repeated this act hundreds of times in the few days following. He did not, could not, eat, make love to, or get preliminary practice for the serious battles of life out of, that sound. But it did give him mental food, mental exercise. The monkey," Thorndike said, "likes to be active for the sake of activity."

As was indicated earlier, no similar observations on monkeys seem to have been made between the date of Thorndike's monograph and the beginning of the work directed by Harlow.

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

At an Ordinary Meeting of the Association held in the Fellows Building of the Zoological Society of London, on Wednesday, 9th February, 1955, to which the Members of the Ecological Society were invited, the following papers were read. The subject of the meeting was "Behaviour and Ecology" and the President, Dr. A. Walton, was in the Chair.

SOME ADAPTATIONS IN THE KITTIWAKE *Rissa tridactyla* TO CLIFF-NESTING

By ESTHER CULLEN

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Most species of gulls nest on the ground. The Kittiwake nests on narrow cliff-ledges and many of its morphological and behavioural peculiarities can be related to this difference. In fighting, a Kittiwake tries to grasp the opponent's beak and twist him off the ledge. The bill has thereby become a strong stimulus, releasing and directing attack. This has modified several threat and appeasement gestures. The use of the Choking display to attract females to the unmated male is probably connected with cliff-nesting. The nest-building technique is unlike that of other gulls for mud is collected and manipulated by specialised movements to form a wide basis for the nest, which may be larger than the ledge it is built on. There are adaptations to keep the nest clean, for the young Kittiwake has to spend longer there than other gull chicks. On the other hand some of the cryptic features of the nest and young of ground-nesting gulls are absent. The behaviour of the young Kittiwake is also adapted to its life on a small ledge. It does not try and run about when frightened, as a young Herring Gull does when placed on such a ledge. The young Kittiwakes possess a broad black neck-band absent in other gull chicks. This structure probably reduces fighting between brood-mates, which might otherwise be disastrous in such a small space.

Unlike Herring Gulls the parent Kittiwakes do not recognise their young.

THE FUNCTION OF EYESPOT PATTERNS IN INSECTS

By A. D. BLEST

Ornithological Field Station, Madingley (*Department of Zoology, University of Cambridge*)

The wings of many insects, notably in a number of families of Lepidoptera, bear "eyespot patterns," circular designs with a remarkably close resemblance to the appearance of the vertebrate eye. They have been evolved independently in wholly distinct taxonomic groups from different morphological structures. It is usually assumed in the literature that these patterns are genuinely mimetic, and serve to intimidate the predators of the insects concerned.

Experiments have been performed to determine whether or not eyespot patterns inhibit attack by small passerines. It has been shown that the display of the Nymphalid butterfly *Nymphalis io* L, elicits escape responses from Yellow Buntings, and that the four large ocelli on the wings are the major releasers for this behaviour. Although most birds become habituated to the displays very rapidly, certain individuals become conditioned to avoid the butterflies altogether.

Experiments with models indicated that the properties of the birds' Innate Releasing Mechanisms for these responses are almost certainly adequate to account for the very exact mimetic resemblances. There is a strong presumption, supported by some evidence, that the birds' responses are inborn.

In the Saturnioidea and Sphingidae it has been found that the presence of eyespot patterns is associated with displays which exhibit them. In addition, correlations between different types of insect display, and the food-seeking behaviour of small passerines are becoming apparent.

A full account of this work, and a discussion of its relation to mimicry theory will appear elsewhere.

THE RESPIRATORY BEHAVIOUR OF THE INDIAN CLIMBING PERCH IN VARIOUS ENVIRONMENTS

By H. SPURWAY and J. B. S. HALDANE

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The koi (*Anabas testvdineus=scandens*) is cultured for food in Indian ponds, and rarely but undoubtedly seen on land. At the Indian Statistical Institute we investigated the frequency of its ascents for air and of its gill movements. The interval between ascents increases with the amount of oxygen in the air or water over a wide range, but opercular rhythm is little affected. Seven per cent. of CO_2 in air did not affect the rate of ascent. In water it doubled it, and 15 per cent. or more completely inhibited gill movements. When fish in oxygenated water breathed an atmosphere of nitrogen, the fish at first ascended for as many as eleven times a minute, as compared with a normal rhythm of about ten per hour; later they stayed below for longer times than when breathing air, punctuated by several ascents in rapid succession

Visual stimuli of various kinds slowed down the frequency of ascent, and a fish unable to find air or gas increased the frequency of its gill movements. If a layer of oil 2 cm. deep is spread on the water the fish repeatedly ascend to breathe the oil. An animal with two alternative methods of homoeostasis not only shows a great influence of minor sensory stimuli, but exhibits behaviour which in other contexts would be called intelligent, when confronted with a novel situation.

STICKLEBACKS AS PREY

By DESMOND MORRIS

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The Three-Spined Stickleback (*Gasterosteus aculeatus*), the Ten-Spined Stickleback (*Pygosteus pungitius*) and the Minnow (*Phoxinus phoxinus*) are all preyed upon by Perch (*Perca fluviatilis*) and Pike (*Esox lucius*). Gasterosteus possesses a few large spines, Pygosteus a greater number of small spines, and Phoxinus no spines. These three prey species were presented to the two predators in a number of different ways; three of the most important results were as follows. (1) In 553 presentations of single prey fish to single predators, Phoxinus was more frequently eaten and less frequently rejected, or avoided, than Pygosteus; also, Pygosteus was more frequently eaten and less frequently rejected, or avoided, than Gasterosteus. (2) Sixty-four sequential tests were made in which single Perch were presented with (*a*) Gasterosteus, (*b*) Pygosteus, and then (*c*) Phoxinus. In 46 of these 64 tests, Gasterosteus was *not* eaten and then (immediately afterwards) Pygosteus *was* eaten. (3) De-spined Sticklebacks were treated as Minnows, and were always eaten.

From these results it can be said that the spines of Sticklebacks protect them to some degree from predation by Perch and Pike and that Gasterosteus is better protected than Pygosteus in this respect. Pygosteus compensates for this short-coming by being more "timid" in its behaviour generally and in restricting its nesting and most of its other activities to the densely vegetated areas of streams, whilst Gasterosteus is bolder, and can afford to nest in the sand, in more exposed situations. The understanding of this basic difference in anti-predator efficiency also clarifies certain other reproductive behaviour differences concerning territorial, courtship and parental patterns.

A BEHAVIOUR STUDY OF DRAGONFLY NUMBERS

The Nature Conservancy, Furzebrook Research Station, Wareham, Dorset

Dragonflies provide exceptional opportunities for ecological and behaviour studies. The aim of the work described is to interpret the density and dispersal phenomena of dragonflies in terms of behaviour.

Density of male Anisoptera on their breeding

areas is rarely more than 9 to 13 insects per 100 yards of narrow stream. Densities higher than this were reduced to the normal maximum by midday on the day they occurred.

This limitation of density results from clashes between males, which cause some of the males to leave the breeding area. Experimental evidence has been obtained to show that the clashes, which are both intra- and interspecific, are primarily sexual and not aggressive: the "beat" of a dragonfly is analogous but not homologous to the territory of a bird. When several species are present together it is members of the smallest species which are displaced.

Recent marking experiments show that Zygoptera in the reproductive stage move about very little if densities are low. Nor do they home to their breeding areas if removed to other waters 200 to 300 yards away. Under certain conditions dispersal of adults in the reproductive stage can be induced by artificially increasing the number of insects at a pond.

Dispersal also takes place in the pre-reproductive stage both at emergence and later. The importance of the pseudo-territorial behaviour in dispersing the species is not known.

BOOK REVIEWS

Progress in the Physiology of Farm Animals. Vol. I. Edited by JOHN HAMMOND. London: Butterworths Scientific Publications, 1954. Pp. xv + 392. 45s.

This is the first of the three promised volumes and provides sufficient material to indicate that the work as a whole will rank as an impressive and useful addition to the literature of animal physiology. As Dr. Hammond points out in his preface, present day textbooks of veterinary physiology are too narrow in scope to provide an adequate background for studies in animal husbandry and production, and stand in contrast to the earlier and broader work of Meade-Smith.

This volume is divided into two sections, "Nutrition and Metabolism" and "Environment," each containing four chapters. There is in any work of this kind bound to be some degree of unevenness in scope or standard between the different chapters, but on the whole the eight contributions are well up to the quality that would be anticipated from each of the authors. Dr. K. L. Blaxter opens with "Ruminant Nutrition" and, although his review is by no means exhaustive, has achieved a remarkable feat in dealing lucidly with so many aspects in a mere 34 pp. Dr. R. Braude's "Pig Nutrition" sets a very high standard of documentation, but Dr. W. Bolton considers that a similar approach to "Poultry" is beyond the scope of a single chapter, and wisely restricts his survey. It is nevertheless a little disappointing that nutritional physiology is so cursorily dismissed. Dr. D. P. Cuthbertson covers a wide range of ground in trace elements and yet presents a most readable account of the major advances in this field. One wonders, however, why the "major elements" have not been provided for except in so far as they may be discussed in other chapters.

The second on "Environment" commences with "The ecology of domestic animals," by Dr. N. C. Wright, which makes most attractive reading and provides a survey of a kind not hitherto attempted. It is unfortunate that references to one or two recent British contributions have been omitted. Drs. J. D. Findlay and W. R. Beakley are responsible for the equally admirable "Environmental physiology of farm mammals," which relates mainly to the environment in relation to heat regulation, and this is followed by a very long but exceedingly useful chapter on "Heat regulation in birds," by Dr. J. C. D. Hutchinson, whose contribution ends with a discussion of the reasons why birds rather than reptiles are used in agriculture, and with the place of climatic research in the adaptation of fowls to undeveloped agricultural areas. Finally there is a chapter on "Daylight changes" in which Dr. N. T. M. Yeates brings together a hitherto somewhat scattered literature in a contribution that will be of particular interest to many readers of this Journal.

A.N.W.

Snakes as Pets. By HOBART M. SMITH. Fond du Lac, Wisconsin: All-Pets Books, Inc., 1953. Pp. vi + 50.

Although a work of this kind would normally receive notice only and not a full review in our columns, it is difficult to let *Snakes as Pets* pass by without complimenting the author, who is Professor of Zoology in the University of Illinois, and the publishers on the amount of information that is simply and lucidly expressed in only 50 small pages. The difficulties of maintaining the only common non-poisonous British snake in captivity obviates the need for a parallel work in this country, but American readers are fortunate in having this volume which, incidentally, includes helpful notes on several aspects of the physiology and general biology of the species dealt with.

A.N.W.

Animal Ecology. By W. H. DOWDESWELL. London: Methuen, 1952. 16 plates and 45 text illustrations. 12s. 6d.

The behaviour of any species can be understood fully only against a background of the conditions under which it lives in the field. Some knowledge of ecology is thus essential for the behaviour student, and Mr. Dowdeswell's book provides an excellent introduction to the subject. In addition to dealing with the special characteristics of land, marine, estuarine and freshwater communities, it covers a host of other topics ranging from mimicry to animal distribution, and from parasitism to the problemg of relict faunae. Although modestly describins itself as suitable for "sixth forms and first year university students," it will certainly find a wider public.

R.A.H.

Bestimmungstabellen der Vorratsschädlinge und des Hausungezefers Mitteleuropas. By HERBERT WEIDNER. Jena: G. Fischer, 1953. 2nd Ed. Pp. 234. Illustrated. DM. 14.50.

These tables and keys for the identification of household and stored products pests cover all the animals which infest houses, granaries, etc., in Europe, i.e. Mammals, Molluscs and Arthropods. An appendix deals with insects which attack wood. The author intends this book for people whose work entails the identification of pests but who may have no formal scientific training. He has, therefore, selected those obvious characteristics which can be clearly distinguished by eye or by using a hand lens, but in the case of the smaller insects the use of a microscope becomes necessary. The major subdivisions are usually to genera or families only, but notes for further identification to species level are also added. Comments on habits are also included, for example, *Rattus norvegicus* and *R. rattus* are distinguished, amongst other characteristics, on their preferences for moist, low places and high, dry places respectively. A book of this sort seems to be needed in England for it is small enough to fit into a large pocket and would be most useful to the growing class of people whose work is to search for and destroy pests.

J.D.C.

The Evolution of an Insect Society. By D. W. MORLEY. London: Allen & Unwin, 1954. 215 pp. 18s.

This book gives an account of Mr. Morley's notions on the evolution of the behaviour of the Wood Ant, *Formica rufa*. It is written in an ambiguous and devious manner, and contains many confusions of both fact and thought, some of which will be discussed below.

Starting with a scheme of phylogenetic relationships which is no longer accepted, he takes as ancestral types *Myrmecia* and *Amblyopone*. This is an unfortunate choice since the latter is degenerate, and the nectivorous diet of the former (which Mr. Morley stresses as a primitive character) is a secondary development. Mr. Morley ignores the more typical *Odontomachus* and *Euponera*, which are carnivorous and do not fit into his scheme.

It is suggested that the success of *F. rufa* is due to an increase in fertility; the large populations made possible only because individuals do more work than in primitive forms. Mr. Morley tries to demonstrate this proposition of increased labour in two ways. Firstly, by comparing the food consumption (in seventieths of a fluid ounce) of grubless colonies of different ants, he claims that a Wood Ant collects three times as much food as a Red Ant of comparable size. The data from which his figures are derived is not available; however, the figures obtained by Holt for food collection by a colony of Wood Ants with brood (which increases food consumption of the colony), work out at less than half that claimed here: moreover since the populations of *M. rubra* are small and variable the figure given for this species could be inaccurate by a factor of two in either direction. Secondly, it is claimed that the more social ants move faster, this being achieved by increasing leg length: the experimental data for this double correlation are not given, and the graph supposed to demonstrate it has no scale on the abscissa.

The brood provide the main stimuli for worker activity. Haskin's work on *Myrmecia* is here misquoted to show that the surface secretions of the young give the releasing stimulus (it is in fact tactile in this ant): but although on p. 68 it is stated that eggs cause foraging, on p. 94 this is denied, while on p. 50 it is stated that the eggs have a dry, hard skin, without secretions, which is supposed to protect them from being noticed or eaten by *nectivorous* parents. The social releasers are supposed to act first on certain hyperactive Wood Ants, called here excitement centres, which Mr. Morley makes the basis of a complex theory of behavioural interaction. Since no experimental analysis has been made, the detailed, factual descriptions of the behaviour of excitement centres in the nest mound, and of their specialisation by habit, have presumably been arrived at by introspection. It is further stated that excitement centres have a high metabolism, the energy from which is largely used up by the brain, which is described (p. 147) as a seething mass of neurons continually moving and changing their shape, size and connections. Such a statement could only spring from the grossest ignorance of neurophysiology.

There are many other errors of fact, and the superficial coherence of the story is attained only by their inclusion, the omission of relevant data and some circular argument. There are some technically excellent photographs, some ill-drawn diagrams (pl. 26, for example, does not confirm its legend) littered with dead ants, and an inadequate index.

D.M.V.

BOOKS RECEIVED

The following books have been received, and in appropriate cases will be reviewed as space permits in early issues:

John D. Black (1954)
Biological Conservation—with particular emphasis on Wildlife
New York: The Blakiston Co., Inc. $5.00

M. L. Johnson, M. Abercrombie & G. E. Fogg (1953)
New Biology, Nos. 15 & 16
London: Penguin Books Ltd. each 2s.

A. S. Romer (1954)
Man and the Vertebrates. Volumes I and II.
London: Penguin Books Ltd. each 3s. 6d.

G. S. Carter (1954)
Animal Evolution. A Study of Recent Views of its Causes
London: Sidgwick & Jackson, Ltd. 30s.

Maurice Burton (1954)
Living Fossils: The Past in the Present
London: Thames & Hudson, Ltd. 21s.

William & Helena Bullough (1954)
Introducing Animals-with-Backbones
London: Methuen & Co., Ltd. 8s. 6d.

Lutz Heck (1954)
Animals My Adventure. Translated by E. W. Dickes
London: Methuen & Co., Ltd. 18s.

H. Hediger (1950)
Wild Animals in Captivity. Translated by G. Sircom
London: Butterworths Scientific Publications. 35s.

M. M. Cooper (1953)
Beef Production
London: Thomas Nelson & Sons, Ltd. 12s. 6d.

H. O. Henderson & Paul M. Reaves (1950)
Dairy Cattle Feeding and Management, 4th Ed.
New York: John Wiley & Sons, Inc.
London: Champman & Hall, Ltd. 52s.

Fougasse (1954)
The Neighbours. An Animal Anthology
London: Methuen & Co., Ltd., for UFAW 7s. 6d.

Harvey L. Gunderson & James R. Beer (1953)
The Mammals of Minnesota
Minneapolis: University of Minnesota Press. $2.00

Clellan S. Ford & Frank A. Beach (1952)
Patterns of Sexual Behaviour
London: Eyre & Spottiswoode (Publishers) Ltd. 22s. 6d.

Karl F. Lagler (1952)
Freshwater Fishery Biology
Iowa: Wm. C. Brown Company. $5.75

Kenneth D. Carlander (1953)
Handbook of Freshwater Fishery Biology—with the First Supplement
Iowa: Wm. C. Brown Company. $6.50

Joseph B. Roberts, Jr. (1952)
Beginner's Handbook of Gold and Tropical Fish
Wisconsin: All-Pets Magazine. 80c.

Harold Bastin (1947)
Freaks and Marvels of Insect Life
London: Hutchinson & Co. 16s.

P. M. Soderberg (1952)
ABC of Cat Diseases
Wisconsin: All-Pets Magazine 85c.

Ernest P. Walker (1954)
The Monkey Book
New York: The Macmillan Co. $4.75

Carl G. Hartman (1952)
Possums
Texas: University of Texas Press $6.00

John F. Breen (1949)
Reptiles, Their Habits and Care
Wisconsin: All-Pets Magazine $1.85

Leonore Brandt (1954)
Raccoon Family Pets
Wisconsin: All-Pets Books, Inc.

Niko Tinbergen (1953)
The Herring Gull's World. A Study of the Social Behaviour of Birds
London: Wm. Collins, Sons & Co. Ltd. 18s.

Francois Bourlière (1954)
The Natural History of Mammals
Translated by H. M. Parshley
London: George G. Harrap & Co. Ltd. 21s.

Monica Shorten (1954)
Squirrels
London: Collins 15s

Duke of Bedford (1954)
Parrots and Parrot-like Birds
Wisconsin: All-Pets Books, Inc. $6.00

Karl Plath, Cessa Feyerabend & Irving E. Altman (1953)
Parrots Exclusively
Wisconsin: All-Pets Books, Inc. $1.25

Mrs. E. L. Moon (1952)
Experiences with my Cockatiels
Wisconsin: All-Pets Magazine $2.00

Colin G. Butler (1954)
The World of the Honeybee
London: Wm. Collins, Sons & Co. Ltd. 21s.

Paul Barruel (1954)
Birds of the World. Their Life and Habits. Translated by Phyllis Barclay-Smith
London: George G. Harrap & Co. Ltd. 60s.

A. W. P. Robertson (1954)
Bird Pageant. Field Studies of Some East Anglian Breeding Birds
London: Batchworth Press. 21s.

A. J. Marshall (1954)
Bower-Birds. Their Displays and Breeding Cycles
London: Oxford University Press (Geoffrey Cumberlege) 30s. (U.K. only)

Jean Delacour (1954)
The Waterfowl of the World. Vol. I
London: Country Life Ltd. 105s.

Joseph B. Roberts, Jr. (1953)
The Pet Shop Manual
Wisconsin: All-Pet Books, Inc. $2.50

Marie Murray (1951)
The Talking Budgie
Wisconsin: All-Pets Magazine 60c.

Cessa Feyerabend (1953)
Budgerigar Guide. Detailed Breeding Methods
Wisconsin: All-Pets Magazine $1.70

Cessa Feyerabend (1951)
Diseases of Budgerigars
Wisconsin: All-Pets Magazine $2.00

Cessa Feyerabend (1951)
The Budgerigar or Shell Parrakeet as a Talker
Wisconsin: All-Pets Magazine $1.80

Cessa Feyerabend (1951)
Modern Feeding of Budgerigars. Better Nutrition Means Healthier Birds
Wisconsin: All-Pets Magazine 75c.

James Fisher (1954)
Birds as Animals 1. *A History of Birds.*
London: Hutchinson & Co. Ltd. 8s. 6d

Robert Stroud (1943)
Stroud's Digest on the Diseases of Birds
Minnesota: Webb Publishing Co. $5.00

O. L. Zangwill (1954)
Psychology as the Study of Behaviour. An Inaugural Lecture
London: Cambridge University Press 2s. 6d

British Poultry Standards (1954)
London: Poultry World, Ltd., and The Poultry Club 25s.

Paul D. Sturkie (1954)
Avian Physiology
London: Baillière, Tindall & Cox. Ltd. 48s.

CORRIGENDUM

Vol. III, p. 40, col. 1. c. 6. The initials of the reviewer of Piéron's *The Sensation: Their Functions, Processes and Mechanisms* are incorrect as printed: they should be E. N. W.

ANIMAL BREEDING ABSTRACTS

This journal covers the world's published research on breeds, breeding, productivity, growth, genetics and reproduction of all farm livestock, poultry, fur bearers and other animals of economic importance, as well as the small laboratory animals. The subject of the review article in Volume 23 No. 1 (March 1955) is "Some effects of improved management on dairy cattle in the tropics."

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BIRD STUDY

The Journal of the British Trust for Ornithology

Edited by H. N. SOUTHERN

Contents of Vol. 2, No. 1, (March, 1955) include *The Breeding of Blackbird, Song Thrush and Mistle Thrush in Great Britain,* Part I, by M. T. Myres; *The Breeding Distribution and Habitats of the Pied Flycatcher in Britain,* Part 2, by Bruce Campbell; *The Summer Movements of Swifts in England,* by David Lack; and *Abrasion and Loss of Rings amongst Sea-Birds.* by J. C. Coulson and E. White.

Bird Study is a quarterly journal intended primarily for publication of the results of the B.T.O's. field investigations and sponsored studies, and of articles to stimulate field research. It is sent free to all members of the British Trust for Ornithology.

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3

THE BEHAVIOUR OF THE DOMESTIC CHICKEN: A REVIEW OF THE LITERATURE

By D. G. M. WOOD-GUSH

Poultry Research Centre, West Mains Road, Edinburgh

Introduction

As an experimental animal for behavioural studies the domestic chicken has had a long but interrupted career. Over eighty years ago Spalding published his work on instinctive behaviour in the chick, and in the first quarter of this century the chick was used by experimental psychologists both in Germany and in the United States. In the last decade its behaviour in relation to agricultural problems has received attention, and the varied interests of the workers has led to a wide dispersal of the literature. It is the aim of this review, therefore, to bring together many of the pertinent references, to present the material critically so that the reader may quickly learn something of the accomplishments and gaps in this field of study. Some papers will have been omitted unintentionally, and not all the papers read by the reviewer have been included, for where a later paper by an author has presented earlier work in a clear and succinct form or repeated the work obtaining the same results, the later work is cited. Furthermore, those behavioural traits used in the diagnosis of pathological conditions have not been discussed.

THE BEHAVIOUR OF THE CHICK

This section deals with the behaviour of the chick until it is no longer brooded.

Prehatching Behaviour

The behaviour of the embryonic chick has received much attention from Kuo (1932a, 1932b, 1932c, 1933, 1938, and 1939). He devised a method for observing the embryo *in situ* by removing a portion of the shell and outer shell membrane, and applying melted vaseline to the exposed inner membrane. With this method he observed several thousand embryos and obtained a detailed picture of the pattern of movements up to the time of hatching. Orr & Windle (1934) and Windle & Orr (1934) unsuccessfully tried to use this method and were compelled to observe their embryos immediately after opening the shell and removal of the shell membranes. Their observations on the sequence of movements generally confirmed Kuo's results. They (Windle & Orr, 1934), examined representative embryos histologically after observing their behaviour, and correlated the embryonic movements with neural development. Some of the responses of the embryo to external stimuli were observed by Kuo (1932a). The egg membrane are torn between 17th and 20th days but in the majority of cases this occurs on the 18th day. Prior to this event the embryo, if removed from the egg to a warm saline solution, generally responds to pressure and touch. After the tearing of the membranes it responds to sound and often to light. Kuo (1932b) observed that hatching only takes place after the onset of pulmonary respiration, and suggests that only after this event has the chick sufficient strength to break the shell. These observations on the condition of the chick and its response to external stimuli offer good material for research into the factors that actually initiate hatching. As yet, no reports on this type of work are to be found, yet the chick embryo, relatively buffered from external conditions and relatively easily observed, offers a fascinating tool to those interested in the development of behaviour.

Hen-Chick Relationships

The primary need of newly-hatched chicks appears to be warmth. Spalding (1873) noted that after hatching, chicks press against anything. Collias (1952) noted that contact with a human hand within 15 minutes after hatching, diminished the distress calls. He also found that there were fewer distress calls from chicks hatched under a lamp than from chicks hatched at sub-normal temperatures. It seems therefore, that the source of warmth need not be specific nor directly tangible for the distress calls to wane. These calls were also decreased by the clucking of the hen, within ten minutes of hatching (Collias, 1952). At this time a moving object had no effect on these calls, but an hour after hatching it caused the distress calls to stop. He also performed tests with loudspeakers and found that clucking has an optimal quality, rate and loudness, and that chicks responded well to far greater rates and amplitudes than those given by a normal hen. Spalding (1873)

was interested in knowing how much of the chick's behaviour was instinctive. He hatched 9 chicks in a flannel bag. At the age of one to two days, they were submitted to the following test individually. They were placed 9-10 feet away from a box containing a hen and chicks. After standing a minute or so they all ran to the hen. Three chicks whose heads had been covered by hoods from the start of hatching and 3 chicks whose ears had been stopped for the first two or three days of life also responded to the noises of the hen when the hoods and stoppers had been removed. It was also found that the instinct to respond to the hen is lost by the age of eight days if the chick has not heard a hen by that age. Bruckner (1933) confirmed this. Collias (1950a) reports that decerebrated chicks will not move towards a clucking or retreating object, but if the basal portions of the cerebral hemispheres are left intact social responses remain.

Evidence indicates that chicks recognize their own dam by various means. Bruckner (1933) showed that hearing is important. A sitting hen was removed in the dark from her chicks and although another broody hen was placed there, the chicks found their own hen. He put two hens with their chicks in a room then one hen was removed and disguised with bandages. When she was returned to the room she noisily tried to divest herself of the bandages and her chicks came to her at once despite the disguise. Collias (1952) also put chicks of different broods together in the dark and found that there was a tendency for the chicks to sort themselves out and to go to their own hens. He says "At least when hens of different breeds are used." It is not clear whether it is still possible when hens of the same breed are used. He also found that visual means of recognition are important. He took chicks from hens of three different colours, and released them in a pen containing 3 hens of the same colours as the maternal hens. The chicks from the black hen went to the black hen; those from the red to the red and those from the white to the white. In his experiments he reports that some of the chicks made mistakes. Bruckner (1933) observes that chicks up to three weeks of age distinguish their own hens after a separation, but older chicks do not give clear cut results.

The problem of whether a hen recognizes her chicks is very difficult, for as Bruckner (1933) points out, the morphological and vocal traits of the chick are continually changing. He suggests that a hen may know her brood by a "complex recognition-impression" of the whole brood. If a strange chick has the prevalent complex marks it will be accepted, but generally a hen will tread on, or peck at, a strange chick. It must have the same habits as her chicks, and the colour of the chick is less important than its habits. If they are more advanced or retarded than the foster brood, it is unlikely to be accepted. He also suggests that a hen may know up to 2 or 3 chickens individually but offers no proof for this. After observing the positions taken by the chicks in the nest he concluded that the hen had no favourites and it was a matter of "first come, first serve."

The importance of vocal communication in the hen-chick relationship is emphasised by an experiment of Bruckner (1933). A chick hidden from its hen gives distress calls and the hen goes in the direction of sound. If however a chick is placed in a glass jar so that no sound is heard, but its actions are seen, the hen takes no notice. If a chick is caught up in cotton threads and begins to call, the hen will run to it and behave as though in danger, and may blindly attack the place. Collias & Joos (1953) with the use of a sound spectograph have made an objective study of the parental signals that attract chicks. They classify these vocal signals into the following three categories: clucking, food calls and the roosting call. Both clucking and the roosting call are stimulated by the distress calls of lost chicks and the roosting call is also stimulated by the onset of darkness. It is a low purring sound. These workers found that these signals have certain common characteristics. They are repetitive; the component notes are brief, and relatively low sound frequencies are found. A similar analysis of the calls of 3 day-old chicks distinguished these types of calls : the cheeps or distress calls, the twitterings or pleasure calls, and the fear trills given when the chick is grabbed.

For the first 10-12 days the chicks are in close contact with the hen (Bruckner, 1933); then they enter a dispersal stage ("Dispersionsstadium"). They now feed independently of the hen but still sleep and warm themselves under her. This stage lasts until the chicks are 6-8 weeks old. The time of dissolution of the brood is variable, and he reports several cases where the brood endured for 12-16 weeks, but usually the hen loses her broodiness earlier, drives the chickens away and joins the other adult birds. The initiative comes from the hen. If the

hen is unable to join other hens she will remain as despot over the chicks until the cockerels mature and dominate her, and if the brood is very small, containing one or two chicks, the hen may tolerate the young birds longer than usual.

Inter-Chick Relationships

Recently hatched chicks do not readily approach one another until they have experienced some minutes of bodily contact (Collias, 1950b). For the first three days there is no competitive spirit (Bruckner, 1933) but it is manifest thereafter. At sixteen days the peck-order fights begin, and the author maintains that once the peck-order is established one may say that the chicks know one another. Guhl (1953) states that the peck-order in small female groups is formed by the tenth week and in small groups when eight weeks old, but there are many exceptions to his statement particularly in male groups where relationships may remain unresolved for many weeks.

Collias (1952) presents evidence of leadership amongst chicks; several groups of 10-12 chicks were tested for response to warmth. They were placed in a narrow run-way with heating lamps at each end, controlled by the experimenter. The chicks gathered under the lamp that was on. When it was switched off and the other switched on, some chicks responded sooner than others, and he reports that a few of these leaders would sometimes repeatedly leave the group under the warm lamp and go to a lagging chick in the cold, and this chick then followed the leader back to warmth. Collias concludes that these data show the leaders to be less stimulus-bound than the others. It is possible, however, that under such conditions many chickens do not correlate warmth with the lamp but with "keeping with the crowd" and this may be a difference between the leaders and the others. Bruckner (1933) however, observed that small groups of artificially brooded chicks appeared to be without leaders. It is possible therefore that certain chicks are precociously sensitive to certain stimuli and act as leaders only when those stimuli are present.

Bückner (1933) kept 2 isolated chicks and when these chicks were seven weeks old, they were introduced to other chicks. One of these "Kasper Hauser" chicks became fully assimilated in three days, but the other was only absorbed after twelve days. He also made observations on the behaviour of chicks to members that are ill, and claims that all chicks, a few days old, show the mania to peck one another's wounds, so that the wounded chick is given no rest. In a brood with a hen there was indifference to a sick flock-member although the hen will often drive a feeble chick away from the brood. Bruckner considers this persecution of an ailing flock-member as an extreme form of peck-order principle, for every chick wishes to establish its superiority over the weakling. It is often trodden by the maturing cockerels and this is possibly due to its "humble" position, which stimulates the cockerels. This aspect of chick behaviour needs further investigation, for it may be of economic importance in artificially-reared broods for the control of disease and conditions such as cannibalism.

The development of aggression and sexual behaviour are discussed in a later section.

Instinct and Learning in the Chick

The early students of chick behaviour were primarily interested in the relative importance of instinct and learning in the activities of the chick. Spalding (1873), some of whose observations have already been quoted, reported that chicks which had been blindfolded from the onset of hatching until the age of 1-3 days instinctively preened themselves and scratched the ground. When given a worm they ran around as though pursued, even if alone. Bruckner confirmed this behaviour in isolated chicks. Spalding also noted that the majority of chicks instinctively showed either fear of stinging insects or at least a suspicion of them. They all tried to catch flies. A newly hatched chick, placed with a turkey chick whose method of catching flies is more efficient, did not alter its method in imitation of the young turkey. However, he reported that some things have to be be learnt by the chicks. They have to learn not to eat their own excreta and he is of the opinion that they have to learn to drink. Lloyd Morgan (1896) observed that chicks never peck at a sheet of water even if they are thirsty and are standing in it. They will, however, peck at any material or bubbles in the water and as soon as the beak is wetted they commence the drinking response.

The development of fear has been reported by several workers. Brückner (1933) found that chicks of less than seven days are afraid of a loud explosion and of loss of equilibrium, although the reaction to the latter factor is not uniform. Spalding (1873) noted that a twelve-day-old chick gave a danger call when a sparrow

hawk flew overhead. Similarly, a week-old brood instantly took cover when a hawk flew over. Distress calls are given by chicks at the approach of any large object (Collias, 1952), although, as state dearlier, a moving object caused the chicks to decrease their distress calls, when they were one hour old. The attachment to human beings or any moving thing by chicks just able to walk was reported by Spalding (1873). He also found that up to the age of three days chicks showed no fear of humans, if kept blindfolded until the encounter, but chicks similarly kept until their fourth day showed great terror of humans. Shepard & Breed (1913) criticized this finding and stated that their chicks kept in the dark for four days or more showed no fear of them, but such docility may have been due to the fact that these chicks were taken from the dark and artificially fed by the workers. That fear is more quickly learnt by chicks brooded by a hen was shown by Brückner (1933). When a rabbit was placed with a hen-brooded group of chicks of less than one week, they showed great fear. An artificially-brooded group of the same age, however, showed no fear, and one chick actually pecked the rabbit. At the age of fourteen days such a group were nervous and at four weeks the chicks went into a wild panic. It seems, therefore, that fear of some things is instinctive and is manifested at a very early stage, whilst fear of other things requires maturation and possibly experience. It is not known whether the chicks of large breeds are less easily frightened than those of small breeds. A thorough study of the development of fear in chicks would be rewarding to workers interested in learnt and instinctive responses.

Spalding (1873) observed that young chicks which had been hooded for their first one to three days, when released onto a sheet of white paper covered with insects, both dead and alive, pecked fairly accurately at the insects within 15 minutes. Swallowing apparently was not so easily achieved. This demonstrated that pecking is essentially instinctive. Since then, the pecking reaction has been studied by a number of workers mainly to ascertain the relative values of maturation and learning in the attainment of pecking proficiency.

The general method used has been to keep chicks in darkness for varying periods and then to test their accuracy at pecking grains. The tests are then continued. In this way it is possible to compare the performances of chicks of equal ages but with varying amounts of practice. More exactly, the tests give the score of the number of misses, strikes, seizes and swallows performed in a set number of pecking reactions. Using Barred Plymouth chicks, Shepherd & Breed (1913) tested and compared four groups of chicks. Two groups had been kept in the dark for three days, the others for four and five days. Data from normally reared chicks used in a previous experiment formed the control data. Tests were repeated up to the twenty-fifth day. Unfortunately, the number of chicks that survived the entire experiment was small. However, the workers drew the following conclusions : in the delayed group the initial records were very low, but the delayed groups rapidly improved during their first two days. Moseley (1925) used larger groups of chicks. Her control group was tested at twenty-four hours then kept in lighted conditions. She had three delayed groups which were tested first after three, six and eleven days in the dark, and then placed in lighted brooders. During their period in the dark, these chicks had been fed artificially in the light. The tests were continued until they were approximately twenty-five days old. Her data showed that normally reared chicks pecked and struck objects with a fair degree of accuracy, from the first. In seizing and swallowing they were inaccurate at the start. In contrast to Shepherd & Breed (1913), she found that the rate of improvement in pecking decreased as the period of delay increased. Cruze (1935) suggests that her findings may be due to the fact that accidentally the chicks had been taught to watch the workers' hands. Furthermore, it suggested that the chicks had to learn a new method of feeding (pecking), and to break the old habit of being fed by hand. Bird (1933) tested four groups of chicks whose average ages were nine, thirty, fifty-one and seventy-two hours respectively. The number in each group was large. The delayed groups were not fed until the first test and after the second test all were given unlimited food. Unfortunately, Bird did not analyse his data fully and some of his conclusions were criticized by Cruze (1935). Furthermore, the use of a nine-hour old group was criticized as birds of this age are generally uninterested in food. In general, Bird concluded that the pecking reactions undergo refinement as the chicks mature and have opportunity for practice. Cruze (1935) had five groups of chicks which received their first tests at twenty-four, forty-

eight, seventy-two, ninety-six and one hundred and twenty hours, respectively. Each test consisted of twenty-five pecking reactions and tests were repeated every twenty-four hours. After the first test the birds were kept in the light and allowed to feed normally although the amount eaten was controlled. The delayed groups were artificially fed. In addition there were three groups, F, G, and H which were returned to the dark after their first test at twenty-four hours. Group F was allowed twelve pecking reactions per day for the entire three week period while Group G were permitted twenty-five reactions per day. Group H was allowed twelve per day for the first 10 days and twenty-five per day for the rest of the test period. During the experiment the weights of the groups did not differ. The data were treated statistically and the author concluded that maturation during the first five days was largely responsible for the elimination of missing errors. The total response, including swallowing, appeared to depend on learning, but more mature chicks develop proficiency more rapidly than younger chicks. The general method employed by these workers, however, has several inherent difficulties. Practice in this context does not just mean practice at pecking but means acquaintance with the whole test procedure, including light. If the delayed groups become more inhibited with the increase in the period of delay then the data obtained would be misleading. Further difficulty lies in splitting the terms "practice" and "maturation" into their component parts.

Summary

1. By examining the chick embryo *in situ* Kuo found that before the tearing of the egg membrane it responds to touch and pressure and, after these membranes are torn, to light and sound.

2. The factors that initiate hatching are unknown.

3. The distress calls of newly-hatched chicks are decreased by warmth and by the clucking of the hen.

4. The instinct to respond to the hen is lost at the age of eight days if the chick has not heard a hen by that time.

5. Chicks recognize their own hen by auditory and visual means but hens generally do not recognize their own chicks individually.

6. The calls of the chick are more effective than its movements, in eliciting aid from the hen.

7. Peck-order fights begin at sixteen days and in small unisexual groups the peck order may be found already formed at eight weeks by males and at ten weeks by females.

8. Some chicks appear to be precociously sensitive to stimuli compared to others and may act as leaders under certain conditions.

9. Young chicks instinctively chase flies in a characteristic manner and avoid some stinging insects. However, they apparently have to learn to drink water and to avoid eating their own excreta. Fear of some things is manifested sooner than for other things and differences in this respect are found between hen brooded and artificially brooded chicks.

10. Pecking is instinctive, but the total action including swallowing improves in accuracy with practice.

THE SENSORY PERCEPTIONS OF THE ADULT BIRD

Vision

Katz and Revesz (1909) reported that they were able to teach birds to distinguish triangles, squares, and circles that had been cut out from beans. Bingham (1913) criticized these results on the following grounds: Katz and Revesz had given no details of the relative sizes of the different forms; the cutting of shapes from beans is very difficult and the birds may have discriminated on the irregularities of the surface rather than on form. There were no control tests in which the forms were inverted or placed at unusual angles. Bingham carefully described his own experimental methods for testing size and form perception in young birds. He found that chicks could discriminate between two circles when one had a 6 cm. diameter and the other had a diameter between 5 and 4.5 cms. As regards form perception his results differ from those of Katz and Revesz. One chick was able to discriminate between a triangle and a circle until the triangle was inverted when the subject became confused. Also when the size of the circle was suddenly increased to more than double the chick made errors. He concluded that the reactions to form are the result of a keen perception of size differences. His work on these factors is undoubtedly very critical but unfortunately his animals became ill and so his conclusions are based on few birds. His conclusion that the chick could not distinguish form was criticized (Hunter, 1913), and he replied to this (Bingham, 1914) main-

taining that two equilateral triangles, one on its base and the other inverted do not differ in form, but in shape. When he inverted the triangle in his experiment, shape was therefore the factor that upset the chick. He also rejected the suggestion that discrimination was by pattern, on the grounds that the discrimination box was dark except for the light on the circle and triangle. In a very good paper, Munn (1931) tackled some of the issues raised by Bingham's work. Using 5 four-month old chickens he was unable to train them to distinguish between a black cross and a black square, of equal area and brightness, both presented on white diamond shaped backgrounds. When two different forms, each on a different background, were used he was able to train four animals to do the problem. When the inner forms were removed the chicks retained a high degree of accuracy. When the background of the positive stimulus—a white triangle—was inverted 3 of the chicks became inaccurate. Similarly when a white square was substituted for the white triangle they became confused. The changing of the negative stimulus did not affect their accuracy. They were apparently responding to "shape" in Bingham's sense, to a differential distribution of light rather than to form. The fourth bird, however, became confused when the negative stimulus was changed but was unaffected when the positive stimulus was changed. In a further experiment, 2 birds were trained to respond positively to a white diamond on a black circle and negatively to a white triangle on its base, on a similar black circle. Both circles were surrounded by white. In some control experiments one or both of the black circles were changed to triangles. In nine control experiments the entire background was black and one or both of the inner forms were changed. The behaviour of the chicks showed that they reacted positively to the point of light in the lower region of the figure (corresponding to the lowest angle of the diamond) and negatively to a straight or relatively straight line of light in the same relative position (corresponding to the base of the triangle). They were apparently uninfluenced by the backgrounds on which the white forms appeared. His conclusions therefore support Bingham's contention that animals do not recognize form *per se* but respond to shape, but contradict the *gestalt* hypothesis, as the animals responded to an element and not to the total configuration.

The visual acuity of the monkey and the chicken were compared under similar conditions by Johnson (1914). The subjects were required to distinguish from a field containing striae each 0.11 mm. wide, another field of broader black and white striae equally wide but whose absolute width could be varied. Two Indian Game Cocks and two Cebus monkeys were used, and it was estimated that the visual acuity of the monkey was four times as great as that of the fowls. He (1916a) trained one of the 2 Indian Game cocks to select a field with thicker regular striae and to reject a field whose only difference was the possession of narrower striae. The bird could discriminate accurately until the difference in the width of the striae was reduced to a value between 33 per cent. and 42 per cent. A Capuchin monkey trained to the same problem showed approximately ten times as much discriminating ability as the bird. These same animals (Johnson, 1916b) were tested to learn what differences in direction of two regular systems of visible striae they could detect. The discriminands were equal in area and brightness. The striae in the positive field were horiztontal and those in the negative field deviated from the horizontal in set amounts, starting at 90 degrees. The cock's difference threshold for direction of the striae was between 25 and 40 degrees while that of the monkey was between 2 and 5 degrees. Johnson, however, points out that "the magnitude of the thresholds within these limits for either individual depends in large part on the effect of training."

Revesz (1924) investigated an illusory space perception in hens. He claimed that the type of optical illusions employed by him, did not permit a purely physiological explanation and depend on psychological factors. When two segments of equal size are placed one above the other, the upper one appears to be the smaller. Hens were first trained to take grain from the smaller. When tested with two congruent segments (see Fig. 1) the hen took grain from the subjectively smaller segment 12 out of 13 times, and, on the next day, 7 out of 9 times. Control experiments were provided by repeating the procedure with objectively different segments. In another experiment the bird was confronted by three figures one above the other. Two were identical and the bottom one was objectively smaller. The bird first took from the objectively smallest and then from the subjectively smaller top one, just as a human

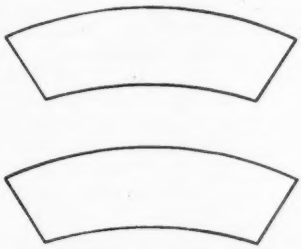

Fig. 1. An optical illusion employed by Revesz in testing the visual perception of the chicken; for details see text.

subject would do.

Another optical illusion used, involves the underestimation of horizontal lines in comparison with vertical ones. When two identical rectangles are placed together, one standing on a short side and the other on a long side, the vertical one appears longer. The hens responded to this illusion. Unfortunately, these experiments were performed with only 2 birds and so really require repetition.

The possession of a high degree of size constancy by fowls was shown by Gotz (1926). He first taught hens to always take the larger of two maize kernels. Then for the critical experiments the two grains of different sizes were placed at various distances and positions from the door where the bird entered. Only one three month old bird was used. No matter where the large grain was placed it was always taken first, showing that the chicken possessed the capacity for size transformation. Further examples of spatial and size discrimination are discussed later, for, as will be shown, they are important clues to the chicken in quantitative assessment.

The most important depth criterion to the chicken was found by Benner (1938) to be shadow. Its position is also important, for his fowls responded to pictures and photographs of peas with good shadowing, but when presented with a picture of peas with shadows in all directions, they showed no interest. Hess, E. H. (1950) was interested to know whether the use of shading, as a cue to depth, is innate or learnt. He reared one group of chicks (the control group) with light from above and another group with light from below. The two groups were then given a critical test at the age of seven weeks by presenting each chick with a photograph of wheat grains, one half of which had been photographed with the light above them and the other half with the light from below. The first peck of each chick was noted. Ninety-five per cent. of the control group pecked at the grains with the light from above while only 4.5 per cent. of the experimental group (reared with the light from below) did so.

The binocular field of the chicken was tested in 13 birds by Benner (1938). One eye of the subject was covered with a shield, and over the head was placed a horizontal, graduated arc with its midpoint corresponding to the midpoint of the fowl's axes of sight. On the edge of the arc was placed a sliding clamp in such a manner that the angle between the mid-point and the clamp could be easily read on the arc. A piece of bait was tied to the clamp which was then gradually moved from the bird's side blind to its field of vision. As soon as the bird saw the bait it pecked at it and the angle between this position of the clamp and the median plane was recorded. The procedure was repeated three times for each eye, and Benner concluded that the fowls have 26° of binocularity. This agrees with Walls' (1942) statement that granivorous birds have a field of binocular vision of up to 25°.

The colour vision of fowls has interested many workers—Katz & Revesz (1909), C. von Hess (1912), Lashley (1916), Hahn (1916), Honigman (1921), Kate & Revesz (1921), Revesz (1922), Katz & Toll (1923), Blasser (1926). For an excellent review on the early work, the reader is recommended to Walls (1942). The nature of the fowl's spectrum was successfully examined by Lashley (1916). He trained his birds to react to red (650$\mu\mu$): yellow (588$\mu\mu$): green (520$\mu\mu$) and blue-green (500$\mu\mu$). He suggested that the fowl's spectrum is divided into not less than five areas of widely different reactive values and that these all correspond approximately to the more conspicuous divisions of the human spectrum. Walls (1942) states that the hen's colour system is trichromatic and probably identical with that of man. The existence of simultaneous colour contrast in fowls was demonstrated by Revesz (1922). His birds were trained to take grain from a green card on a grey background. When given a grain on a contrast green that was produced by a grey card on a red background it was accepted, but grains on grey cards with other backgrounds were refused. Katz & Revesz (1909) claimed to have demonstrated the presence of the Purkinje effect in fowls, and Lashley (1916) whose methods are much more

critically presented, suggested that there was some "slight evidence" that the phenomenon may be present in fowls.

Colour constancy in the chicken was found by Katz & Revesz (1921). Their birds were trained to accept white rice grains and to refuse grains dyed red, yellow, green or blue, when these were offered on a coloured base. After training, white grains on a white background were lit with coloured light so that the grains had the appearance or being dyed, and the birds readily accepted them. Kohler (1918) showed that they also have a high degree of brightness constancy, for his fowls after being trained to discriminate between two grey cards of differing brightness, later reacted not to a particular grey but to the brighter or dimmer card, in accordance with their training.

Kroh & Scholl (1926) sought to discover whether form or colour was the more important in the consideration of an object. A fowl was taught to take grains of cereal from blue circles and to leave those on red triangles. When the grains were offered on red circles and blue triangles the bird took from the blue without hesitation. The general applicability of this finding, however, will probably be modified by the action that is under observation, as well as by the experience of the individual bird and the particular stimuli used.

The aiming and pecking ability of fowls with a moving target and restricted field of vision was tested by Katz & Keller (1924). They employed a revolving stage, with grain scattered on it, whose speed could be regulated. With the stage stationary a hen pecked at the rate of 3.5 times per second, and this pecking did not alter when the stage moved at 13 cms. per second. When the stage movement was 33 cms. per second it pecked at 1.8 and 2.0 times per second and stopped entirely when the stage was speeded up to 66 cms. per second. At medium speeds the bird followed the grain with small jerky movements and the authors suggest that optical orientation follows only between single jerks. When the field of vision was decreased to 22.5 cm. $\times$ 15 cms. the pecking efficiency decreased; with the grain appearing on the bird's right and disappearing left and with movement at medium speeds, the bird pecked once per second; when it had to face the oncoming grain it pecked nine times per second but when the grain moved away from it, the bird refused to peck at all. Benner (1938) found that when pecking at a stationary grain fowls generally aim at 5 mm. below the actual grain and he calculated that this constituted an eight per cent. error in the total striking distance.

The ability of five weeks old chickens to discriminate between two directions of horizontal movement was tested by Stavsky & Pattie (1930). The three subjects learnt to respond positively to a kymograph moving from right to left, and to respond negatively to one moving from left to right. It was found that when the chicks could only see one of the discriminands, they acted correctly showing that they had learnt to respond to both stimuli correctly.

Although artificial lighting affects the productivity of chickens, very little is known about the effect of light on its behaviour, and what is known is presented incidentally in the literature. Guhl (1953) reports that birds start feeding when the light is one foot candle and begin to peck one another when it is two foot candles. Nothing is known about their behaviour on very long days, compared to short days.

Taste

The taste sense of birds has received some attention. Hellwald (1931) fed hens bread soaked in quinine solution (1 : 500) and in pure water respectively. All the bread was equally accepted no matter in what order the samples were given. With drinking liquids, however, different results were obtained. The birds were presented with two identical drinking bowls, one containing pure water and the other containing quinine solution. More pure water was taken and the quinine solution was eventually abandoned. Engelmann (1943) and (1946) reported on very similar experiments. He classified taste into four component qualities:—salt, acid, sweet and bitter. He found the birds to be very insensitive to bitter solutions. when he used quinine or magnesium chloride. They accepted a 0.24 molar solution of magnesium chloride with a frequency of 67.0 per cent. $\pm$ 9 per cent. in contrast to 100 per cent. acceptance of pure water. With sodium chloride dissolved in water they accepted 0.50 molar solution with 83 per cent. $\pm$ 4 per cent. frequency and an 0.60 molar solution with 31 per cent. $\pm$ 3 per cent. frequency. When hydrochloric acid was diluted in water they even accepted 4.0 and 5.0 molar solutions with a frequency of 17 per cent. When offered a choice between wheat grains soaked in magnesium chloride (5.0 molar solution) or soaked in water, the birds took both in equal frequencies. Similarly with grains

soaked in a 5.2 molar solution of sodium chloride. When tested with grains soaked in 1.4 molar solution of hydrochloric acid, they soon refused to accept either the treated grains or the control grains. In the case of sugar solutions he (1946) reports an interesting result. The birds preferred the sugar solution to pure water, but this preference apparently depended on the viscosity of the solution, for when a bitter solution was increased in viscosity artificially, it too became preferred to water. Engelmann therefore concluded that in fowls the tactile sense is more important than taste and that they only really recognize three taste qualities, but he does not mention any experiment in which sweetened but less viscous solutions were offered to the fowls. It is evident from these experiments that the taste sense of the chicken is not acute, but the physiological processes whereby any taste discrimination takes place is unknown for there are no taste buds (Bradley, 1950). It is suggested by Sturkie (1954) that they possess a chemical sense rather than true gustation. An experiment by Hellwald (1931) indeed suggests that they may possess such a sense. He starved 8 hens of calcium for nine days. They were then put into two groups, both of which were fed macaroni, but in the macaroni of one group small bits of egg shell were hidden. In the afternoon after this feed, both groups were placed in front of piles of egg shells. The group that had received none in its morning feed took 91 grams while the other group took 27 grams. When he repeated the experiment a week later, similar results were obtained. Of course, an explanation of these results involving the use of tactile sense organs of the crop is not precluded by Hellwald's experiment. The ability of chicks to choose adequate diets under certain conditions will be discussed in a later section.

The Other Perceptual Senses

The visual senses of the fowl have been more fully investigated than any other perceptual sense, yet apart from their colour vision, we know remarkably little. Furthermore, many of the experiments were performed with very few animals and since the temperament of the subject can influence the results to a large degree, repetition of much of the work is desirable. Also in many of the earlier German papers the lack of clarity in describing methods and lack of statistical treatment warrant cautious acceptance of their conclusions. Shadow has been shown to be important in the perception of depth but we know nothing of the other monocular cues to depth and distance in the case of the chicken. Neither do we know how a chick learns to judge distance nor even its limits to depth and distance perception. Movement perception is an important factor to a bird yet the critical frequency of the fowl remains unknown. Even the behavioural effects of light from a practical economic viewpoint remain unknown. Less, however, is known of the other perceptive senses. The sense of smell of the fowl is generally assumed to be poor but there does not appear to be any critical assessment of it in the literature. The auditory and tactile senses of the fowl also do not appear to have been property investigated, despite the fact that the tactile sense is thought to guide the bird in forming food preferences.

The sensitivity of the fowl to temperature has received some attention, while the effect of the other interceptors on the behaviour of the fowl do not appear to have been analysed. Robinson & Lee (1946) describe the behaviour of White Leghorns and Australorps at high temperatures. When body temperature reaches 108°F. the first effects of heat become apparent, the birds pant and stand with wings partly outstretched. The White Leghorn drinks large amounts of water whilst the Australorps drink sparingly and retire by themselves. When the body temperature reaches 113°F. the birds find difficulty in breathing, and collapse. Hutchinson & Sykes (1953) working with Brown Leghorns found that birds which were tolerant to hot climates became less active in the heat but if they were intolerant to heat they became very excitable at 111°F.

Summary

1. Chickens do not recognise form *per se* but can discern differences in shape and size.

2. In discriminating between two figures they respond to an element of the figure rather than to the total configuration

3. Hens respond in the same way as human subjects to optical illusions involving figures that differ only subjectively in size. However, they possess a high degree of size constancy.

4. Shadow is a very important cue to deph perception and its use as a criterion to depth is learnt.

5. The binocular field of the chicken is 25°—26°.

6. The fowl's spectrum is divided into not

less than five areas that correspond approximately to the more conspicuous divisions of the human spectrum. Its colour system is trichromatic and it possesses the faculty of simultaneous colour contrast and both colour and brightness constancy to a considerable extent.

7. When pecking at a stationary grain, fowls generally aim at 5 mm. below the actual grain.

8. Five week old chicks learnt to discriminate between two directions of horizontal movement.

9. Chickens start feeding when the light is one foot candle and begin to peck one another when it is two foot candles.

10. The taste sense of birds is very poor and the tactile sense appears to be more important in determining food preferences. Possibly they possess a chemical sense.

11. At very high temperatures, behavioural differences between breeds are found.

INTELLIGENCE AND MEMORY

Katz & Revesz (1909) taught a number of hens to pick only one of two types of cereals offered to them, individually, on a board. Ten grains of each cereal were offered. Each bird was tested until it made ten correct pecks with no mistakes. The number of such trials was counted. They were then tested after various periods to see if they had retained any of this knowledge. One hen tested after four weeks made only two mistakes. Another hen after six weeks made 25 wrong pecks compared to 27 when she was just introduced to the problem. Whether such differences between hens are due to differences in mental ability or merely due to temperamental differences cannot be decided. Katz & Toll (1923) also performed experiments to test the memories of 5 hens. The birds were also taught to differentiate between two types of grain one of which was glued to the board. Three days after their training the birds were again tested and most of them took the correct cereal first, but then tried to take the forbidden one. The birds showed differences in the rates at which they learnt but the differences were probably temperamental differences, as the "cleverest" hen was described by the workers as being the most "confiding"! These birds were given other tests such as finding food in simple mazes. Nearly a month later the authors tried to conduct an experiment to find out whether the birds were capable of a primitive form of counting. Of the grains placed on a board every second grain was free and the others were glued. Three of the hens immediately found the solution to the test by recognizing the stuck grains, which is probably a better indication of memory than the data of the previous experiments. When it was repeated later, hiding the glue with dust, the birds solved the problem and the authors suggest that they did it by obtaining an impression of density and spacing. Katz & Revesz (1909) had come to a similar conclusion when the experimental animals solved the problem of every third grain being stuck. No bird however solved it when every fourth grain was stuck. Honigmann (1942a) suspected that in this particular set of experiments the birds were able to distinguish the glued grains. He therefore repeated the experiments under conditions as similar as possible and achieved the same results. He then applied the crucial test of having all the grains loose and the birds ate them all. Eventually he did train his birds to take every second grain in the critical test, but he eliminated the training error of Katz & Revesz. He used a different type of grain eliminating shade differences between fixed and loose grains and also a heavier base was employed so that each peck did not cause the loose grains to shake. He found great differences between individual birds. Most important was his analysis of the significance of spacing to the birds in solving this problem. When the distances between grains were altered suddenly from the standard distance used in training, the bird failed, but when the distances were changed gradually, the birds successfully pecked alternate grains. The same results were found if the distances between grains in a row were made unequal. He noted that the birds showed no preference for odd or even grains when pecking the alternate grains in a loose row, and using more critical methods than Katz & Revesz had employed, he was unable to train birds to leave every third grain untouched. Modifications of experimental conditions such as introducing a different coloured ground surface caused the animals to give negative results at first, but they soon underwent a "spontaneous re-adjustment" and resorted to alternation without further training. One of his hens after an interruption of five months gave perfect results after 99 experiments. compared with 550 experiments necessary at her introduction to the problem. This feat of memory

is all the more surprising when the paltry reward for correct trials and the lack of punishment for mistakes are considered. Revesz (1922) presented a cock with another problem in which the bird had to distinguish between varying amounts of food. This animal is reported as preferring three grains to two, four to three, five to four, six to five, eight to six, and ten to seven. The author reports the same results whether the grain was arranged regularly or irregularly, horizontally or vertically. This result agrees with the conclusion drawn by Bingham that chickens are able to discern small differences in size. Similar experiments with other animals showed that the limits varied with the individual but this again may be due to differences in temperament between the subjects.

With the exception of Honigmann (1942a) these workers do not give enough information on the methods used and statistical precision is lacking. Also in many cases there appears to be negligence of possible clues that may guide the animal and permit the workers to make wrong interpretations. For a critical appraisal of many earlier experiments on number conception by animals the interested reader is recommended to Honigmann (1942b). The information at present shows that the fowl is able to learn alternation and to distinguish between quantities that differ very slightly. Their space perception and size discrimination are responsible, in part at least, for their ability to do so.

Differences in the methods of learning of a single problem by chicks are displayed in the data of Munn (1931). Three of his experimental animals learned to discriminate correctly between two stimuli by responding only to the positive stimulus, for when this was changed they became confused. Alternation of the negative stimulus did not affect their accuracy. A fourth chick learnt the problem by responding to the negative stimulus only. Stavsky & Pattie (1930) found that their chicks learnt another problem involving two stimuli, by responding to either stimulus.

Revesz (1924) found that if the grains that a fowl was pecking were covered with a sheet of paper, the bird gave up pecking. He interpreted this as meaning that the bird retained no visual representation of the food that had lain in front of it, as a human subject would have done.

The memory of the fowl under more "natural" conditions has been reported upon by several workers but those references referring to the remembrance of flock-mates will be referred to later when the peck-order will be discussed.

Schjelderup-Ebbe (1923) stated that a hen could remember such things as a hole in the wire of the pen, roosting perches and nesting places for a long time, but did not cite any specific examples. Their memory of food-stuffs and places was investigated by Engelmann (1951). He fed stinging nettles to young chicks which learnt in one day to avoid them, but after four days they had forgotten and accepted them readily. Adult fowls could only remember them for eight days. Sour dock was remembered for fourteen days by adults. Five-and-a-half-month old fowls after being away from their usual run for fourteen days, remembered their former feeding place. Another group of 3½-month old chickens forgot the geography of their run after three weeks absence. He maintains, however, that sounds are more readily remembered than visual impressions and that chickens can remember a food call for thirty days. Older hens were found to remember a stall after thirty days absence; one hen remembered after fifty days absence but after sixty days away none remembered. Unfortunately, in these experiments he generally gives no indication of the amount of individual variation.

Engelmann (1951) suggests that retention of certain factors in the fowl's memory depends on the type of stimuli involved. The work indicates that auditory stimuli are more important than visual ones under certain conditions, and further investigation along these lines should prove interesting. His suggestion that there are breed differences in the ability to remember flock mates also provides a fruitful field for investigation.

The susceptibility of chickens to hypnosis was studied by Gilman, Marcuse & Moore (1950), who found that as birds became tamer and more used to the procedure, their susceptibility decreased but increased if the procedure was suddenly changed. The authors suggest that fear and disrupted stimulus-reception are interactive in evoking immobility.

Summary

1. Chickens are able to learn alternation, i.e., picking up every other grain in a row, and the ability to do so depends partially upon space and size perception.

2. The same problem can be learnt in different ways by chicks, for some may respond only to

the positive stimuli, others only to the negative stimuli. In some experiments they may respond to both.

3. Young chicks which had learnt to avoid stinging nettles forgot them after four days. Adults forgot nettles after eight days, and sour docks after fourteen days. Five-and-a-half month old birds remembered their runs after fourteen days absence and older birds may remember it after thirty days away. Calls are probably remembered for a longer period.

4. Hypnotic immobility in chickens is probably due to an interaction of fear and disrupted stimulus-reception. Increasing tameness and acquaintance with the procedure decreases their susceptibility.

THE "LANGUAGE" OF THE CHICKEN

It has been suggested that the crowing of the cock is a territorial call and serves to attract females (Collias & Joos, 1953). Katz & Revesz (1921) made recordings of the crowing of a certain cock over a long period. They found that he crowed essentially the same melody. Pitch remained constant over a 2-4 hour period but varied from day to day by a whole key. The duration of each crowing remained very constant for successive crows but varied slightly from day to day. Crowing by normal, untreated hens was reported by Schjelderup-Ebbe (1923) and by Guhl, Collias & Allee (1945). The one hen observed by Schjelderup-Ebbe was the dominant hen of a flock containing no cock and she seldom laid eggs. The other hen he observed crowing was old; had stayed with her chicks for a long time and had become very masculine. He reports that the head and neck movements of crowing hens is very similar to cocks but the call is hoarse. The onset of crowing in different groups of cocks was also reported by Schjelderup-Ebbe (1923). There were three groups each containing 30 young male chicks. One group was totally isolated from adult birds; the second group could hear adults and the third group lived with adult birds. He claims that the second and third groups crowed before the first group. No statistical treatment is given and also it is not clear whether these groups were observed throughout the day. If observations were of limited periods, then the times recorded will probably be the maximum and not the minimum times. Hamilton (1938) treated 2 day old chicks with testosterone propionate, and sixty hours after the start of treatment they began to "crow." Similar results were obtained by Noble & Zitrin (1942). Hamilton states that by the 27th day after the start of treatment the crowing had acquired a diphrasic pattern in that there were at least three distinct tones and, like the call of the cock, the crowing could be modulated from high tones and back again. These experiments indicate that crowing is instinctive, but do not show that the "song" itself is entirely instinctive.

Schjelderup-Ebbe (1923) analysed the calls of adult birds and concluded that each sex has ten calls. This analysis was done by ear and is in need of objective treatment with a sound spectograph. An objective analysis of this nature has been given by Collias & Joos (1953) to the warning calls of chicks and adult birds. These workers divide these calls into five categories; those given in the presence of aerial predators; those given to ground predators; fear squawks given when the bird is caught; the alerting call given by the broody hen and the threat calls of cocks which apparently vary in pitch between cocks, and finally the crowing of the rooster which serves to warn other males. All these warning signals are of relatively long duration and possess relatively little segmentation or repetition. Furthermore there is an absence of or lack of emphasis on very low frequencies. The calls that attract chicks were also analysed and have been mentioned earlier.

This accurate method of analysing animal calls open up opportunities for studying the relative roles of learning and instinct in the "language" of the chicken. Nevertheless until we know something about their hearing ability our knowledge of inter-chicken communication must remain very incomplete.

Summary

1. In the crowing of the cock pitch remains constant for 2-4 hours but varies from day to day by a whole key. Crowing has also been observed in normal hens.

2. Two-day old chicks treated with testosterone propionate started "crowing" sixty hours after treatment.

3. The warning signals of chickens are of relatively long duration and possess little segmentation or repetition and there is an absence or lack of emphasis on very low frequencies.

THE FEEDING HABITS

To anybody who has handled poultry it is

obvious that the birds have preferences for particular foodstuffs, but this phenomenon has received little scientific attention. Engelmann (1940) found that his birds were very fixed in their preferences for cereals and had a strict preferential order as follows: wheat > maize > rye ~ barley > oats. When these cereals were presented to the same fowls in ground form, wheat, rye, oats and barley were eaten at the same frequencies. Ground maize and ground peas were less popular, and Engelmann suggests that this was due to the fact that maize and pea meal are crumbly, less compact, less easily eaten than the others and different in colour. He also carried out a series of experiments with artificially made grains. When "wheat" and "rye" grains were made from rye meal, the "wheat" grains were significantly more popular. When "rye" grains made from wheat meal were presented with "rye" grains derived from rye meal, both were equally popular. In a third series he presented "rye" grains from wheat meal and "wheat" grains from rye meal and found the "wheat" grains were significantly more popular. Finally, when "wheat" grains from rye meal and real rye grains were offered, the "wheat" grains were preferred. He dyed wheat, maize, and rye grains, and peas, in eosin. At first the fowls refused them but after one day's hunger they accepted them. Not all the colours were identical and no check on brightness was made. The order of popularity remained, after the fowls had learnt to accept them. The natural coloured maize was more popular than the dyed while the dyed peas were generally more popular than the uncoloured—the poor taste sense of the fowl suggests that these preferences were based on colour differences. When the ground forms of the five cereals and peas were dyed and artificially made to look alike, they were all accepted at equal frequencies. He concluded from these experiments that the birds formed preferences on the basis of form and colour with the possible aid of tactile impressions but not by taste. Ewing (1947) states that they prefer food with shining or glittering surfaces, and it is unfortunate that Engelmann did not include this factor in his experimental procedure. Unfortunately apart from Engelmann's work there appears to be none other in the literature analysing the basis of food preferences of the fowl. Using chickens that had never seen grain, Engelmann (1942) found that they had an initial and probably innate preference for elongated grain forms rather than for rounded forms such as peas. The first grains they took were rye grains but after some experience they, like his adult fowls, preferred wheat grains. Collias (1952) suggests that the selection of feeding stuffs is partly learnt from the parental example. A young chick pecks wherever the hen pecks and will peck at a lettuce leaf that it had formerly neglected if the leaf is tapped with a finger.

Bayer (1929) studied the food habits of 19 fowls. He also found that they had food preferences, but unlike Engelmann found that preferences of individual birds varied. He attempted to learn whether the amount set before a hen had any effect on the amount eaten. From the data given, it would appear that the greater the pile of food set before the hen, the more she eats. He also tested the hens to see if they preferred large grains of a cereal to small grains of the same cereal. When he fed them whole and broken rice grains, they took the whole grain, but he does not say whether they had previously been conditioned to recognize the small grains as rice or not. When hens were offered a mixture of wheat and rice they were reported to have eaten more than if offered only one cereal and when three foods were mixed the intake was greater still. When three foods were offered singly, 100 grams of each, more was eaten if the most popular food was given last, rather than first. The re-offering of food, if it was fairly popular, led to an increase in consumption. The appetite of a bird could also be increased by taking away the food at intervals or by introducing another hungry bird.

The free selection of foodstuffs from a limited range by young chicks was observed by Funk (1932) and Graham (1932) and by Dove (1935). Funk found that the choice of foodstuffs during the first two weeks after hatching did not conform to their later choice. Graham found that his chicks had no marked choice in the first week or ten days of life which may mark the period of learning. Funk reported that the choice of his chicks corresponded very closely to the standard diet given at that institution. However, he fed them cod liver oil in their drinking water. Graham (1932) found that chicks hatched in the winter took significantly more cod liver oil than those hatched in the late spring. None of his chicks showed common complaints generally attributed to nutritional difficulties. Dove (1935) found that it is possible to predict the growth of a

chick over a two week period from its growth over the previous two weeks. He divided 100 chicks into groups of 10 chicks each on the basis of their predicted growth, so that the groups formed a graded series from the fast growing group to the slowest growing. The chicks were allowed a choice of seven foodstuffs and were weighed bi-weekly, predicted growth rates being calculated. Ten control groups were kept and each was fed the rations selected by one of the experimental groups. The control group that was fed the ration selected by the fastest growing group, grew at a significantly greater rate than the control group fed the ration selected by the slowest growing group. Unfortunately Dove gives no indication of the amount of changing of chicks in his experimental groups, so that one has no idea whether the tendency to select well, persisted or not.

Graham (1934) described the food consumption of three groups of pullets over a period of fourteen months, and of 6 individual pullets over a period of thirty weeks. The birds took an adequate diet, and they had some individual preferences; their intake of individual foodstuffs varied from day to day and week to week.

The evidence, so far, is that birds are able to select a good diet, but there is no evidence how this is done. Moreover in all cases the foodstuffs offered were restricted and no detrimental ones were offered. The offering of a foodstuff poor in nutritive value but made attractive according to Engelmann's observations on the basis of food preference, would be an interesting study. Recent studies, (Heywang, 1946), have shown that better growth is made by chicks in hot climate if fed during the cooler part of the day. No evidence is available on the effect of climate on the feeding behaviour of birds with free choice. Furthermore nothing is known about the relationship between the time of feeding and other activities.

Summary

1. Birds have very marked food preferences which are most likely formed on the basis of form and colour with possibly the aid of tactile impressions.

2. Young birds initially prefer elongated grain forms to round ones, and the selection of feeding stuffs may be partially learnt.

3. The more food set before a chicken the more it will eat, and if it is given a number of foodstuffs singly, it will eat more if its favourite foodstuff is given last rather than earlier in the sequence. Its appetite is also increased by removing food or introducing a hungry bird.

4. If given a free selection of feedstuffs birds are able to take an adequate diet, although there is some individual variation.

THE PECK-ORDER

Introduction

Since Schjelderup-Ebbe's early reports (1922, 1923, 1924) on the social hierarchy of chickens, many observers have substantiated his descriptions. It is now recognized that the peck-order forms the basis of all group behaviour in adult chickens, and immediately after a meeting between strange hens, the contests begin.

He (1922) reported observations on small groups of 2-25 birds and on large groups of 25-100 birds, and concluded that when more than 10 hens are present, linear hierarchies are rare, and "triangular" and "square" relationships are common. In a typical triangular relationship, bird R pecks bird S who pecks bird T who is dominant to R. Masure & Allee (1934) substantiated Schjelderup-Ebbe's observations on the domestic fowl and compared it to the type of social hierarchy found in pigeons. They also described a group of 11 six-month old cockerels whose hierachy contained six triangles and which still had two relationships unsolved after seventy days observation. Schjelderup-Ebbe (1922) also found that some flocks possessed despots; others had "Cinderellas" and birds lower down the social scale were generally more cruel to their inferiors than birds higher up the scale. If such a bird was transferred and obtained a higher position it became more tolerant. Guhl (1953) found evidence of a peck order in a flock of 96 White Leghorn pullets, although not all the pecking relationships were known. Fischel (1927) found that under range conditions, birds formed apparently loose groups when away from the hen house, and that these groups were led by any hen.

Murchison (1935a, b, c) tried to describe the social hierarchy of chickens in terms of a social law based on the concepts of time, space, and their subsidiary categories. He tried to identify simple quanta of social phenomena that could be measured in terms of time and space. The first of these was 2 individuals moving towards one another and he called this "social reflex No. 1". He identified two more

social reflexes,—the second being two individuals fighting to a conclusion, and the third he described as the sex reflex. He used a very small sample of birds in very artificial conditions and some of his original generalizations have failed to be substantiated (Guhl, 1942).

The Formation and Duration of the Peck Order

In small groups of female chicks a peck order is formed by the tenth week, while male chicks form one by the eighth week (Guhl, 1953). In the same paper Guhl compares the peck-order formed by 11 chickens reared together and the one formed when the same birds are re-introduced to one another as strangers. These results were also compared with the data obtained from two sets of pair-contests. For these contests the birds are at first isolated and then after a suitable time they are introduced into a neutral area, for the contest. This paired contest technique was also used by Allee, Collias & Lutherman (1939) and by Collias (1943). A low and non-significant correlation coefficient was found to exist between the ontogenetically determined peck-order and the final peck order. When the birds were introduced into a pen statistically significant correlations were found to exist between (1) number of birds pecked in the ontogenetic peck order, and the number of contests won in the first series of pair-contests; and (2) between the two sets of paired encounters; and (3) between the second set pair encounters and the final peck order. Guhl concluded that if the relative aggressiveness of individuals in a flock is to be assessed, more than one of the above-mentioned criteria should be used. He also cites other experiments in which the ontogenetic peck order of three flocks was compared with adult peck order after similar treatment. In two flocks the correlation coefficients were non-significant. The small number of flocks used does not allow any generalizations, but suggests that factors other than aggression or strength can affect a bird's status. Schjelderup-Ebbe (9922, 1935) had noted that the results of encounters between hens were not always resolved by either aggression or strength. If one bird is afraid there is no fight and the other is victor; if both are frightened the first to overcome its fear is dominant. He also noted that the fighting ability of a bird can be affected by its physiological state at the time of the encountered, thus a fatigued bird might lose to a bird that it would normally beat. If a hen is introduced into a flock, several birds might attack her at once and all become dominant to her regardless of their individual abilities. Birds on strange territory are less pugnacious than birds on home territory and the bird on its own ground has greater prospects of winning an encounter with a stranger. Collias (1943) analysed statistically the factors which make for success in initial encounters. He controlled the variables of sex, territory and numbers present, by using only White Leghorn females, two at a time on neutral territory. He measured the size of each bird's comb, using it as an indicator of the amount of male hormone present. The weight of the bird gave an indication of "strength," "impressiveness" and general health. Its rank in its home flock was used as indicative of "the psychology of success." Also the state of moult of the winning bird in each pair was compared to the state of moult of the loser. Each of these measured factors was correlated with success by means of the path coefficient method. Their order of importance was found to be: absence of moult, comb size, social rank and weight, but the author concluded that these factors as measured and used in the analysis accounted for only about 56 per cent. of the factors involved, and suggested that more accurate indicators possibly may have given higher values for the paths, and thus decreased the importance of residual factors. Age did not appear to be important, but experience in winning or losing was.

Further factors suggested by Collias are differences in fighting skill, chance blows, differences in sensitivity to hormones, wildness, mild indisposition, past history of the individual, slight differences in handling, errors in judgement and resemblance of opponent to a former despot. This last mentioned factor was found by Potter (1949) to be important, for in comparing the dominance relationships between different breeds she found that some hens would behave in a characteristic manner to their opponents' breed rather than to their opponents as individuals. The possession of a large comb was found by Guhl and Ortman (1953) to have psychological value in paired contests. Three pullets, that had been least successful in paired contests with 8 other pullets, were given large dummy combs and after suitable isolation were allowed to meet the other pullets. They won more encounters than previously and were generally avoided. After another suitable period of

isolation the same pullets were paired again. This time there were no dummy combs and the 3 pullets reverted to their previous positions.

Once it is established the peck order may endure unchanged for months in small flocks of about 10 birds. In larger flocks it is less stable (Guhl, 1953), and revolts by individual birds against specific superiors are likely to happen. Revolts have been caused by hormonal injections (Allee, Collias & Lutherman, 1939). It is therefore possible that some revolts may be due to slight endocrine changes. Guhl (1953) suggests that under range conditions the peck order of large groups may be less stable. This may be due to the fact that birds may forget one another when contact is infrequent, and it is most likely that the rebellious bird in a small, long established, penned flock, offers a different sort of problem.

The Physio-Psychological Basis of the Peck Order

The physio-psychological basis of the peck order has been discussed by Allee, Collias & Lutherman (1939) and Collias (1944). These workers suggest that it depends firstly upon factors that determine the birds' position such as aggression, and secondly on those factors that maintain the *status quo* such as memory, and "habit reinforce," which may replace aggression. As a start, Allee and his colleagues have investigated the effect of various hormones on the aggressive behaviour of birds. Allee, Collias & Lutherman (1939) investigated the effect of testosterone propionate on the social position of birds. In a number of small flocks whose peck orders were well known, several birds low down in the social hierarchy received amounts varying from 0.25 mg. — 1.25 mg. daily for 7-8 weeks. Their behaviour was observed daily for 3-5 hours. It was found generally that the larger the dose, the more rebellious the birds became. The revolts at first were against birds low in the peck order, but later superior birds were overcome and high positions gained. Amongst the controls receiving sesame oil injections daily, no social changes occurred. The workers were unfortunate in that a large number of birds died during these experiments and their numbers were therefore small. It is interesting to note that long after the treatment had been terminated and the overt effects of the hormone had vanished, the birds still retained their new positions. Similar psychological factors were observed by Hale (1948) when the alpha females in two flocks retained their positions after debeaking.

Nine birds from four flocks, some of which had been used in the experiments above, were injected with oestradiol, to test its influence on the peck order (Allee & Collias, 1940). Only two changes in social position were observed and in both cases the treated birds lost to social inferiors. A poulard receiving 1.0 mgm. daily for 18 days crouched to the workers within three days of treatment while a control poulard struggled to escape. The next day, the treated poulard crouched to a cock while the control remained entirely dis-interested. Staged combats in neutral pens during the treatment indicated that the treated birds had lost aggressiveness. The authors tentatively conclude that treatment of over 0.3 g. daily for long periods decreases comb size and egg production, but they admit that the observations are based on too few cases. Thyroxin as influencing the peck order was investigated by Allee, Collias & Beeman (1940). Observations were carried out daily for five months. In the first series of injections 4 birds were given 5-7 mg. at each dose and 3 of those that received more than one dose died. All moulted severely. In the second series 2 birds received doses of 3-4 mg. every fourth day, one bird getting three such doses and the other 11. In the final series, 10 birds received 0.25-2.0 mg. every fourth day, and the doses varied in number from 4-12. In neither the second or third series were there any changes in the social positions of the birds. In one bird, given both testosterone and thyroxin simultaneously, the effect of testosterone was not diminished. The birds in series two and three moulted slightly and it is of interest to note that the moulting did not affect the peck order in these small flocks.

Guhl (1950a) set up two small experimental flocks of 1 cockerel, 5 capons and 6 pullets, and 1 cockerel, 4 capons and 7 pullets respectively. The capons varied in the size of comb that they possessed. Five had very small combs, 2 had combs intermediate between the small combed capons and normal males and the remaining 2 had combs larger than the 2 normal males. On autopsy these 4 large combed capons were found to possess remnants of testes and 5 were without testicular material. The peck orders that were observed were ontogenetically determined, for the birds had been reared together. Generally the capons were dominant to the females but 2 exceptions

occurred. In one flock 1 female pecked 4 capons including a capon with an intermediate comb. In the other flock 1 small combed capon was pecked by 4 females. These abnormalities may have been due to the origin of the peck order and it would be interesting to see the peck order of a flock of capons and hens determined with adult birds, and the results of paired encounters before flock formation.

The position of the poulard in a peck order is less definite. Normally the hen possesses a left functional ovary and a rudimentary gonad on the other side. Domm (1924) and (1929) reported that a large number of birds that had had their left ovary removed between the ages of six weeks and six months became indistinguishable from capons. Some became relatively pugnacious and attacked cocks introduced into their pens. Examination by autopsy revealed the presence of testicular tissue in the formerly rudimentary gonad, and he reported (1929, 1930) spermatogenesis in similarly ovariectomized birds. Collias (1944) states that when the ovaries were removed from 6 pullets selected from various positions in a flock of 12 birds, the operates were relegated to a lower status than the intact birds but retained the same social ranks relative to one another. He does not state whether these birds had both ovaries removed or only one. If only one ovary was removed these results in contrast to Domm's larger sample could be due to incomplete ovariectomy or to ovary regeneration or even to the length of observation, for the growth of testicular tissue is slow. Bilaterally ovariectomized pullets are unmasculine, relatively inactive and non-combative (Domm, 1929). The presence of gonadal tissue in the hen appears to be necessary for the display of aggressive behaviour. The social status of intersexual birds was reported by Domm & Davis (1938). These workers injected oestrogen into Brown Leghorn eggs on or before the fourth day of incubation. The resultant intersexual birds constituted a graded series with the most feminine group being nearly indistinguishable from normal females. Their gonads were ovotestes and commonly a left and often a right oviduct was present. The birds with the most masculine plumage were near the top of the peck order and those with the most feminine were at the bottom. Females that had received this treatment and these intersexual males formed an intergrading peck order unlike the normal situation in a pen with normal males and females, which form two distinct peck orders.

An experiment designed to investigate the inheritance of aggressiveness was described by Guhl & Eaton (1948) and Guhl, (1953). Unfortunately, the experiment yielded no clear cut results. The ontogenetic development of aggression has received very little attention. Collias (1950c) suggests that fighting may develop from frustrated sexual behaviour in young males. No reports are to be found in the literature on individual differences in the rates of development of aggressiveness, nor on the plasticity of the trait.

Potter (1949) attempted to ascertain whether there were differences in social dominance between birds of different breeds. She used twelve small flocks containing 1 or 2 birds of each breed: Light Brahma, Rhode Island Red, White Wyandotte, White Leghorn, Brown Red Game, Brown Leghorn and White Cochin Bantam. The White Leghorns were significantly more dominant than the others. Game hens were dominant to all the others except the Rhode Island Reds which did not differ from the White Wyandottes or Brown Leghorns. The Rhode Island Reds were dominant to the Light Brahmas and Bantams, while the White Wyandottes, Brown Leghorns, and Light Brahmas were dominant to the Bantams. An analysis of variance of the ranks achieved by all hens in all flocks showed that the differences in ranks held by the different breeds were significant. Certain differences in fighting methods were discernible. Fennell (1945) found that Game Cocks tolerated more punishment, were faster and more nimble than hybrid cocks of domestic breeds, and that the methods of attack used by different Game Cock races varied.

As previously stated, the maintenance of a peck order implies the recognition and memory of individuals. Schjelderup-Ebbe (1923) stated that birds usually fight one another after a separation of two weeks, and suggested that this was due to the fact that they had either forgotten one another or had forgotten their dominance relationships. Engelmann (1951) removed a hen from her pen for two weeks and then returned her. She apparently remembered the pen and went straight to the food dish. Her pen mates were aggressive, but she apparently remembered them, for she submitted to her previous superiors and fought only with her previous inferiors. In order to learn something about methods of recognition between hens Schjelderup-Ebbe (1923) disguised some animals

and shortly afterwards returned them to their pens. The combs of the birds were turned to hang on the side opposite to the usual one and these birds were attacked. In another experiment the combs and wattles were stained with violet, white, blue, black yellow, red and green. Those treated with blue and black were attacked, and so, to a lesser extent, were those dyed with green or violet. Yellow caused the hens to peck at it. Guhl (1953) noted that when a dubbed bird was returned to her pen after two days, together with a control pen-mate, she was attacked but the control was accepted. The dubbed bird attacked her inferiors but submitted to the challenge of her superiors. A flock of dubbed birds formed a peck order, showing that factors other than the comb help in the recognition of the individual. Guhl & Ortman (1953) extended Schjelderup-Ebbe's work on disguising birds from small, well-integrated flocks, and used as his criterion of recognition the acceptance of the bird without any challenges from members of the flock. Changes to tail, wings, saddle back and breast by the addition of ordinary or coloured feathers, or by denudation, evoked no challanges except where black or green had been used. Alterations to the head, neck or comb were more effective in this respect, but duplicate disguises did not always give the same results. He concluded that deportment appears to be an important stimulus for aggression, for a bird in a strange environment behaves in some manner detectable by the others which attract them. Engelmann (1951) makes exactly the same point. In these experiments the threshold of attack appeared to be very variable and many of the 59 tests were inconclusive. Many of the attacks recorded were by inferior birds only, which raises an interesting point. Douglis (1948) reported that when new birds were introduced into a flock, in 14 per cent. of the cases the alpha resident bird was the first to challenge the stranger, and in 36 per cent. of the cases it was the second bird to do so. Therefore it is surprising that a considerable number of Guhl's disguised birds were challenged by inferior birds only. Guhl concludes that the recognition of the individual does not depend on a limited area of the body or on a single feature.

Douglis (1948) investigated the peck order in flocks which contained part time members (certain hens that were put there for fixed periods at regular intervals) and in flocks that were entirely part-time. Assimilation of new birds into a flock generally took about three days if the bird was dominant, but sometimes took as long as five weeks. Continuous presence with flock mates does not appear to be essential for the maintenance of status in the flock hierarchy, provided the part time member is present at intervals. The length of the longest possible absence consonant with flock membership was not determined, nor was the minimum time present. Birds that were isolated when not "visiting" were less easily assimilated. In most cases resident birds did not change their relationships to one another with the introduction of visitors.

Guhl (1942) wished to determine whether social discrimination extends beyond the individual so that a bird reacts to a socal position, rather than to the individual. He used a discrimination pen similar to that used by Murchison (1935a). A bird is released into the pen which contains 2 other birds caged on opposite sides of the pen. The released bird was considered to have discriminated when it paused within one foot of one of the caged birds, but no qualitative differences in the type of discrimination were noted. In one flock 35 per cent. of the releases resulted in no discrimination, in the other flock there were 53.4 per cent. non-discriminations. He was unable to substantiate the earlier claims of Murchison (1935a & b) and concluded that his birds did not discriminate between social positions as such. In all tests discriminations appeared to be influenced by the individuality of the subject.

Hale (1948) investigated the effect of debeaking on the social hierarchy. Five debeaked hens formed a peck order but showed a considerably higher peck frequency than the control flock. However, the peck of the debeaked birds seldom elicited a response from their inferiors. In 48 paired encounters between debeaked and normal birds, the operates won 29, including 12 fights. Debeaking did not lessen social tensions. No reports are available in the literature on the effect of "glasses" on social tension.

The Effect of the Peck-Order

Since the peck order forms the basis of all social behaviour in chickens its effect on the individual has been reported by several workers —Colias (1944), Guhl (1953), Guhl, Collias & Allee (1945). High ranking birds have priority for food, nests, roosting places, and greater freedom of the pen. Guhl & Allee (1944) compared well integrated flocks with an estab-

lished peck-order to flocks undergoing constant reorganization. The criteria used for the comparisons included the amount of pecking, food consumption, maintenance of body weight, rate of egg production, size of comb, seniority and social status. It was found that generally the hens in the organized flocks pecked each other less than in the experimental flocks. Food consumption was higher in the organized group than in either the experimental flocks or isolated birds. When feeding was restricted the controls maintained body weight better than birds in the experimental groups. The controls produced more eggs than the experimental groups. Comb sizes measured weekly, roughly followed the same trends as egg production. When the experiment flocks were altered by removing the bird with the longest residence, it was found generally that each newcomer entered the flock as the omega bird and emerged as the alpha bird. These results which were obtained over a period of 13 months indicate the value of the social order to the flock as a whole, and the necessity of social cohesion for good production, but as the authors state, further work is necessary and it is suggested that similar studies should be performed using heterosexual flocks, and taking fertility as a criterion of success. The relevant papers on the effect of the peck order on mating behaviour are discussed in the next section.

Summary

1. The peck-order is the basis of all group behaviour in adult birds. In large groups linear hierarchies are rare, and "triangular" and "square" relationships are common. Evidence of a peck-order was found in a group of 96 birds.

2. The "ontogenetic" peck-order is not always correlated with the peck-order found when the same birds are re-introduced as adults.

3. The winning of contests does not depend upon the bird's aggressiveness entirely. Other factors of importance are the conditions under which the birds meet, and their state of health. A number of other minor factors have also to be considered.

4. In small flocks the peck-order may endure for a long time, but revolts against superiors do occur and can be induced by testosterone propionate injections. Some of the birds receiving oestradiol injections lost their positions, but moderate doses of thyroxin which caused the birds to moult, did not alter their peck-order positions.

5. Generally capons are dominant to hens, and poulards that have had only one ovary removed may likewise be dominant to hens, but bilaterally ovariectomized poulards are relatively non-combative and inactive. Intersexual birds vary in aggressiveness according to their degree of masculinity.

6. Significant differences in the social positions attained by birds of different breeds were found in small flocks, and certain variations in the methods of fighting were discernible between breeds.

7. After two weeks absence birds are apt to forget one another.

8. The disguising of birds sometimes causes lack of recognition by pen mates. Changes to head, neck or comb are more effective than changes to tail, wings, saddle back or breast by denudation or addition of feathers. However, the recognition of the individual does not appear to depend on a limited area of the body or a single feather.

9. Assimilation into a flock takes from three days to five weeks and a bird may belong to a peck order without continually being present.

10. Debeaking does not prevent the formation of a peck order and the frequency of pecking actually increases after debeaking.

11. High ranking birds have priority for food, nests, roosting-places, and greater freedom of the pen.

12. Hens in well organized flocks, compared with hens in flocks whose social order was kept in a constant state of flux, ate more food, produced more eggs, and maintained body weight when feeding was restricted.

MATING BEHAVIOUR

The Cock

The mating behaviour of the chicken has received much attention in recent years as it is extremely pertinent to the poultry industry. The frequency of mating in the fowl has a well defined diurnal rhythm. Upp (1928), Skard (1937), Parker, McKenzie & Kempster (1940), Penquite, Craft & Thomson (1930), Long & Godfrey (1952) all report that the maximum number of copulations takes place in the late afternoon, but as yet no explanation for this factor has been given. The possibility that psychological factors may affect this rhythm

was shown by Skard (1937). One cock was allowed to copulate in the mornings only for three days, then he was released with the hens for the entire day. On the two days following his morning releases he copulated more in the morning than was usual. Needless to say, this experiment needs repetition before any conclusion can be drawn. This cock observed by Skard copulated 53 times on his most active day, but whether these were all complete matings is uncertain. Many matings result in no cloacal contact and if even such contact is made there may be no ejaculation by the male. Parker, McKenzie & Kempster (1942) fitted a semen collector to cocks under observation and reported that 14 per cent. of apparently normal matings resulted in no semen in the collector. This figure may be rather high, for their cocks which were released for only 15 minute periods may have been over-excited. Furthermore, the collector gave consistently lower yields of semen than manual massage (Parker, McKenzie & Kempster, 1940). These same workers in their 1942 paper state that males copulate as often as 41 times in a day. When Penquite, Craft & Thompson (1930) observed the matings of 6 Small Comb White Leghorn cocks placed singly with a number of females, from 6 a.m. until 6 p.m., the number of copulations varied from 28 to 6. After a mating the hen was removed and all her eggs over the next 16 days were set. The number of fertile matings varied from two to eight, and bore little relationship to the total number of matings. The figures on fertility do not take account of the reproductive condition of the hen and therefore do not accurately reflect the maximum fertility of these males alone, for Parker (1945) found that the presence of a hard shelled egg in the "uterus" lowered the fertility of the females. Another factor to be considered is the removal of a hen after one copulation, for it is very probable that under normal conditions a cock will mate with some hens more than once. It seems unlikely however that the number of hens fertilised in a day will much exceed the numbers given by Penquite *et al.* Considering the number of sperm per ejaculate and the number necessary to ensure high fertility, Parker *et al.* (1942) conclude that the number of hens a cock could fertilize in a day is about the same number quoted by Penquite and his co-workers. Burrows & Titus (1939) claim that semen production and libido are uncorrelated in the chicken and the figures given by Parker *et al.* (1940) would also suggest this, but more evidence is needed. The possibility that high libido and high fertility are incompatible is also put forward by Parker *et al.* (1942) on the grounds that the male may copulate too frequently to allow sufficient sperms to accumulate. Guhl & Warren (1946) found that some of their hens that mated frequently tended to lay infertile eggs. Once again, however, the matter needs further investigation. Rasmusson (1952) selected two lines of Albino rats, one a line of high sex drive and the other a line of low sex drive, and he found that the low line had significantly higher fertility.

The fertility and hatchability of the eggs is higher when the hen is inseminated in the afternoon (Parker, 1945, 1950). He concluded that the hatchability was higher when there was a soft shell egg in the uterus compared to when there was no egg or hard shelled egg in it. He did not attempt to correlate these facts with events in the cycle of ovulation.

Polge (1951) found that cocks varied in their semen production; density varied with the individual, and from time to time. He also found seasonal variations in 12 White Leghorn cocks. Volume increased between November and December and declined from January to August, when the minimum volume was produced. Density increased slightly in winter, reaching a maximum in March and then declining until September. He was also able to obtain semen from his cocks when they moulted. Parker *et al.* (1942) found that the mating rate declined in September but as each of their males was only observed for 15 minutes per month their data must be accepted with reserve. Wood-Gush (1954a) noted that the rate of courtship of Brown Leghorn cocks declined when they were moulting. Parker *et al.* (1940, 1942) found that cocks kept in battery cages were less active sexually than males penned with hens. However, due to the small number of observations this finding should be accepted with reservation, for the caged birds may have been over excited. Hays & Sanborn (1939) found that fertility declined with age in cocks but with hens the relationship between age and fertility was less marked. The effect of age on behaviour *per se* has not been investigated. Parker & Bernier (1950) found that the optimum ratio of males to females was 6-7 males per 100 hens.

Long & Godfrey (1952) investigated the effect of environmental temperature and dubbing on the mating behaviour and fertility of cocks.

Pairs of brothers from different breeds were used so that their progeny were marked genetically. One member of each pair was dubbed. No difference between the dubbed and undubbed cock's mating behaviour was found. Temperature had no effect except when a cock's comb and wattles were injured by freezing.

The courtship of the adult cock has been described by Skard (1937) and Wood-Gush (1954a). While Skard's observations covered most of the day, Wood-Gush's were of short duration, nevertheless their descriptions of the cock's actions are similar, although Wood-Gush has described a larger number of actions including displacement reactions. However, neither worker attempted to classify all the calls of the cocks during their presence with the hens. Wood-Gush found that in the short observation period each cock performed certain actions at fairly characteristic frequencies. He also found that under these conditions the hens crouched to the cocks at different rates but was unable to relate this to the behaviour of the cocks alone. Guhl, Collias & Allee (1945) had earlier observed that hens did not treat all cocks alike. Guhl (1951) using a certain number of courtship actions of the cock as an index of courting behaviour, showed that the courting rates of the male were not always related to the response of the females. He found significant differences between the rates at which the males copulated. His observation periods were very short, sometimes as little as nine minutes, so that any cocks which were slowly stimulated would have been handicapped. Differences in the rate at which cocks copulated had been reported earlier by Guhl, Collias & Allee (1945) and by Penquite, Craft, & Thompson (1930), and Skard (1937). The two earlier workers observed the cocks for long periods at a time, and there is no doubt that differences in rate of mating do exist between cocks. When several cocks are put into a pen together dominance relations complicate the picture. Guhl, Collias & Allee (1945) found that the dominant cock did most of the mating and prevented the others from mating although he might be tolerant to a certain inferior. When the alpha cock was removed the other cocks did not tread often although they had been vigorous mating cocks prior to competition. The authors conclude that the inferior cocks had been so conditioned as to be "psychologically castrated." They also concluded that the social position of a male and his sex drive are not necessarily related—an important point from the view of the practical breeder. Guhl & Warren (1946) found that the dominant cock in each of two experimental groups sired the most chickens, and this was confirmed by Godfrey & Long (1952).

The Hen

The mating behaviour of the hen was classified by Skard (1937) into ten actions grading from acceptance of the cock to complete avoidance. In the light of so much work on avian mating behaviour over the last fifteen years, the work probably needs repetition and elaboration, for the generally passive role of the female makes interpretation difficult. Guhl, Collias & Allee (1945) observed the mating of White Leghorn hens in small flocks. They found a significant negative correlation between social rank and the frequency of mating. In other words, hens higher up the social hierarchy mated less than their social inferiors. Similarly hens high up in the social hierarchy were courted less than their inferiors, and in some flocks the high ranking hens crouched less than the other hens. A significant positive correlation was found between the rate at which a hen was courted and the rate at which she was mated. In some flocks a positive correlation was found between the number of sex invitations and number of matings.

Guhl (1950a) formed two heterosexual experimental flocks, already described as consisting each of 1 cock, several capons and hens, in order to determine the influence of the social dominance of the males over the females upon the success of mating. The normal males dominated the capons who, with a few exceptions, dominated the hens. Most of the treading was done by the normal males and the more masculine capons. Later two of the inferior capons were given oestrogen injections to increase their sexual activity but not their aggressiveness. After this treatment they trod and courted at relatively high rates, but mostly with socially inferior females. Superior hens often repulsed the small combed capons when they tried to mate and Guhl concluded that although a male may mate with superior females, social dominance of the male facilitates mating. He (1950b) investigated further the influence of high social rank upon the receptivity of the hen. In these flocks the high ranking hens crouched less than the lower and middle ranking hens, although hens showing relatively high and low receptivity were found at all levels of the

dominance orders. He then subdivided each flock into three levels of dominance and separated the three sub-flocks. The same males were used and rotated between the sub-flocks. The high-ranking hens now crouched more frequently than, or approximately as much as, the hens forming the lowest level. In two of the sub-flocks the middle and low-ranking hens crouched less after sub-flocking than before it. These results show that hens, like cocks, differ in their sexual activity and that psychological factors resulting from the males present, and their own social rank, influence their sexual activity.

Surprisingly little attention has been paid to the relationship between the egg production of the hen and her sexual receptivity. Collias (1950c) cites some unpublished work by Heuser done in 1916 showing that over a four-week period the correlation coefficient between individual mating frequency and egg production was $0.610 \pm .11$. Lamoreux (1940) found that in a six-week period covering the peak of production over a period of five years, the fertility of the eggs increased with the intensity of production. The larger clutches had the higher percentage of fertile eggs. He favours increased sexual activity with a high rate of ovulation as being the reason for this high percentage of fertile eggs in large clutches; and offers the work of Heuser & Wilkins (both unpublished) as proof. The observations of these workers cover only a few days. Both these workers scored frequency of mating which is really not a good criterion of female sexual activity for it depends on the cock as much as the hens, and the sexual invitations or crouches might also have been considered to advantage. Furthermore, there is later contradictory evidence. Upp (1928) observed a small flock for 16 days and found no relationship between egg production and number of matings. Guhl & Warren (1946) suggested that hens with high sexual activity tend to lay infertile eggs. No evidence is given by Lamoreux to preclude the possibility of high rates of ovulation being correlated with superior internal conditions for fertilization, or some such physiological condition. Evidence from mammals tends to show that oestrus behaviour and ovulation are not inseparable (Robinson, 1954).

Preferential Mating

Upp (1928) observed a flock of birds daily for two periods of three days each and later repeated another test over 16 consecutive days. He found that the cock showed a definite preference for certain hens and could not discern any action on the part of the hen to account for it. Hens that followed the cock around continuously were often neglected. Wood-Gush (1954a) showed that some hens crouched significantly more for one cock than two others. Some of the examples of so-called preferential mating, e.g., Warren & Kilpatrick (1929) can be explained on the grounds of differential sexual activity of the males. In this particular case males with genetic markers were put in with females for fixed periods, the eggs set, and the table of matings drawn from the results of incubation. If certain females had no progeny by a cock it was deemed a case of preferential mating. However whether any preference in the sense that Upp describes, had indeed been effected, is doubtful.

Unisexual Matings

Abnormal unisexual matings have been reported from many sources. Adult females may assume the male role (Guhl, Collias & Allee, 1945), Guhl (1948), and tread other hens. These hens usually lay normally and Guhl (1948) suggests that social dominance facilitated these unisexual matings but emphasises the need to discover the conditions which evoke the behaviour. He (1950a, 1953) also describes unisexual matings in flocks of males, in which high ranking males trod their inferiors, but no voluntary receptivity by males was noted.

The Castrates

The mating behaviour of castrates provides an interesting avenue for the study of the role of hormone in relation to mating, and on the effects of learning and other psychological factors in the sex drive. Domm (1927) describes the complete castrate as generally being negative in its sexual behaviour, but in those cases where the castration has been incomplete, he describes their behaviour as being similar to the normal male but milder in form. Guhl (1950a), as already described, used large and small comb capons in a mating experiment. The large comb capons courted and mated more frequently than the small comb ones. Autopsy on the large comb capons revealed the presence of testicular material, but in the five small comb ones no testicular material was found. Nevertheless they courted and trod, albeit at very low rates. Poulards that have had the functional ovary removed, may develop an ovo-testis on the right hand side. These birds which look masculine may tread normal hens (Domm, 1927).

Goodale (1918) describes male Brown Leghorn birds that had their testes removed and ovaries implanted. He obtained two types of birds. Type one had well-developed spurs, but comb and wattles similar in size to the normal hen and their plumage was feminine. In type two the plumage was variable. The first type of bird trod normal hens and crowed.

The intersexual males obtained by Domm & Davies (1948) through injecting oestrogen into fertile eggs before incubation were divided into four classes according to their degree of feminity, the fourth class being nearly indistinguishable from females. The least feminine birds copulated with normal hens while the most feminine only waltzed weakly to normal hens and did not tread. They avoided a cock while the least feminine attacked it. Only one of 22 intersexual males was found to be sterile. Females that had received the prehatching treatment were found to crouch for the rooster if they laid eggs and to avoid him if they were non-layers.

Hormones and Mating Behaviour

That some elements of male mating behaviour are innate has been demonstrated by the administration of hormones to young chicks. Hamilton (1938) injected 500 gamma of testosterone propionate daily into chicks from the second day after hatching. Crowing started 180 hours after the first injection, and wing-flapping, which Wood-Gush (1954a) suggested to be a form of male display, was much in evidence. Noble & Zitrin (1942) extended this work. They started their treatment when the chicks were 12-15 days old and also included some birds that were reared under isolation. Crowing started within two days of start of treatment and by the 13th day treading had begun, but no cloacal contacts were observed. The isolated chicks were equally precocious. These workers also injected 12-15 day old female chicks with oestrogen and by the 28th day of treatment all treated females had been observed to crouch to males while the control females would not tolerate the males. However the workers were unable to repeat the results of this experiment with oestrogen. Collias (1950c) states that he found testosterone propionate 13 times more effective in inducing male behaviour in male chicks than was alpha-oestradiol-benzoate. Domm & Van Dyke (1932a) using hebin, a gonad-stimulating hormone, induced young males to tread at 13 days of age after ten daily injections. Crowing started after six daily injections. Similar treatment on young female chicks produced no overt behavioural effects although there was considerable hypertrophy of the ovary (Domm & Van Dyke, 1932b).

Koch (1936) claimed to have increased the fertility of normal White Leghorn cocks by giving them androgen treatment. Unfortunately he used only 4 cocks, 2 of which received treatment. 88.6 per cent. of the 482 incubated eggs from the pens of the treated birds were fertile, as opposed to 43.6 per cent. of the 361 incubated eggs from the control pens. If one of the controls was naturally of low sexual activity, similar results could have been obtained without the treatment. The author did not test the fertility of the cocks before treatment and so no valid conclusions may be drawn from the experiment.

The effect of androgen treatment on the sexual behaviour of normal Brown Leghorn hens was observed by Domm & Blivaiss (1947). Out of 24 birds receiving subcutaneous implantation of testosterone, 3 birds were found to copulate in a male manner, and several crowed and waltzed. Many of the birds were treated at different ages and no clear cut reason for the differences in response can be given. Daily injections of testosterone propionate caused capons to crow and copulate vigorously (Davis & Domm, 1943); when these workers gave oestrogen injections to capons they copulated in a male manner but did not crow. Guhl (1950a), as mentioned earlier, increased the rate at which his small comb trod and courted by oestrogen treatment. When Davis & Domm treated two normal roosters with stilboestrol they lost their aggressiveness, and ceased to crow, but still continued to copulate although their courtship apparently was not vigorous. Three bilaterally ovariectomized poulards when treated with testosterone, became aggressive, crowed and waltzed to normal hens. However, they never trod the hens which crouched to them, so that it is not certain whether they exhibited sexual behaviour as such, or merely aggressive behaviour. Oestrogen treatment on such birds generally caused them to crouch for roosters. Poulards whose left ovary had been removed, on receiving testosterone, became more aggressive but never trod. From these observations it is seen that the male mating action including treading can be induced in both sexes and in the various castrates, but female mating behaviour has not been artificially induced in males or capons.

Lamoreux (1940) injected normal hens and pullets with oestradiol benzoate daily for eleven days. On seven of these days males were introduced for 4-5 hours, but the rate of copulation remained low. His dosage given in rat units was large and is likely to have upset the birds (see Allee & Collias, 1940). Furthermore, half the birds were not yet in laying condition or had gone out of lay for reasons unspecified, so that any conclusions must be very tentative.

The effect of thyroxin on the mating frequency of hens was tested by Collias (1946). Large doses (2.0—4.0 mgm.) caused the birds to moult. Low or moderate doses depressed sexual activity and he suggests that his was due to increased nervousness and sensitivity of the skin.

Summary

1. The mating behaviour of chickens possesses a well defined diurnal rhythm with the majority of copulations taking place in the late afternoon.

2. An active cock may copulate forty or more times a day but the number of fertilizations may be small, and it is suggested that a good cock will fertilize approximately 8 females per day.

3. The fertility and hatchability of eggs is higher if the hen is inseminated in the afternoon.

4. The production of semen varies with the individual and in the same individual from time to time. There is also a well defined seasonal effect on semen production which declines in August and September.

5. The cock has an obvious courting behaviour.

6. Marked individual differences in the rate at which cocks mate have been found under many conditions. When in competition, the dominant cock may prevent the other cocks from treading, and the libido of these cocks may decline.

7. The social dominance of the male facilitates mating, but aggression and libido are not necessarily related.

8. Hens high in the social hierarchy generally mate less than their social inferiors, and are courted less. However after some flocks had been subdivided into three levels of dominance, and the subflocks separated, it was found that "high-ranking" hens crouched more frequently or as much as the hens in the lowest level.

9. Evidence on the relationship between the egg production of the hen and her sexual activity is contradictory.

10. Preferences of cocks for certain hens and of hens for certain cocks have been reported.

11. Unisexual matings have been reported for both sexes, and although some females may voluntarily assume the male role, there are no reports of a male voluntarily assuming the female role.

12. Capons if sexually active perform in a male manner, and the frequency and intensity of their mating depends on the amount of testicular material present. Poulards that have had the functional ovary removed and appear masculine, may tread normal hens.

13. The implantation of ovaries in castrated males did not induce female behaviour.

14. Some elements of the male courtship may be induced in young male chicks by hormone administration.

15. Testosterone propionate given to normal hens induces aggressiveness, and some of these hens may court, and others copulate, in a masculine manner.

16. Male mating behaviour can be induced in both sexes by hormones, but female mating behaviour has not been induced in males or capons.

NESTING BEHAVIOUR

Scant attention has been paid to the nesting behaviour of the chicken. Turpin (1918) carried out observations on small comb White Leghorns, White Plymouth Rocks, and Rhode Island Reds, using open nests, while Wood-Gush (1954b) observed Brown Leghorns, using trap nests. Turpin found that approximately 72 per cent. of the laying hens left the nests by one o'clock. He found that prior to choosing a nest the birds sat on several. The length of time on the nest was also found to vary. Wood-Gush also reports that the birds visit several nests before choosing one, and that the time spent on the nest before oviposition varied from one hour to three hours forty minutes. His birds were also very conservative in the choice of a nest. He found that young birds were very restless and nervous before laying and called a great deal. In a group of 11 young pullets starting to lay, 4 laid all their eggs in nests; another 4 at first laid on the pen-floor and subsequently nested; 3 however never used the nests during the period of experiment (and continued to avoid the nests for the rest of the laying year—

Unpublished). Wood-Gush suggests that the general nervousness of the female before laying would have a selective advantage in the wild by acting as an incentive to the bird to find a safe nest. The persistent floor-layers he suggests, did not respond to the stimuli of the trap-nests, for they never examined them as the other birds did. Turpin (1918) carried out some experiments on the stimuli of nests. A hen's egg made a nest more attractive to the hens than a china egg, but wooden nest eggs and home-made plaster of paris eggs were superior to the hen's egg in this respect. Concealed nests were more popular than open nests. The problem of egg soilage was investigated by Hansen, Bearse & Berg (1948). They tried different types of nest litter, but found no relationship between nesting materials and egg soilage. Straw, excelsior, and wood fibre were preferred by the birds to wood shavings, rice hulk, almond shells, diatomaceous silica pellets, and Douglas fir bark cork particles.

Cole & Hutt (1953) reported that in ovulating non-laying hens nesting was a common occurrence. Wood-Gush (1954b) found that some of his hens although released after laying would return to the nest and spend the major part of the day there. They were not being persecuted and were not broody. He suggests that the ruptured ovarian follicle which plays an important part in the time taken to lay may also control the nesting drive, and that psychological factors may also play a part in determining the time spent on the nest.

Summary

1. Hens visit several nests before choosing one; they are very conservative in their choice.

2. The time spent on the nest varies.

3. Where trapnests are used some pullets accept them readily while others if untrained neglect them entirely.

4. Birds, particularly young pullets, are very nervous before laying and this may have had a selective advantage in the wild.

5. Wooden nest eggs and home made plaster of paris eggs in a nest make it more attractive to a hen than a nest containing a hen's egg, which in turn is more attractive than a nest containing a china egg.

6. Concealed nests are more popular than open nests.

7. It has been reported that ovulating but non-laying hens commonly nest.

BROODING BEHAVIOUR

Pearl (1914) was one of the earliest workers to pay attention to broodiness as a subject for scientific investigation. He analysed the records of 850 Barred Plymouth Rock birds over a period of seven years. Once a bird was classified as broody she was confined to a detention coop and when the symptoms disappeared she was returned to the flock, a method that is widely used in commercial enterprises. He found that broodiness is cyclic in occurrence and, in some birds, may occur 4-5 times from March to June, but is not confined to one season. The degree of intensity may vary in the same hen. Hellwald (1931) paid attention to the food intake of three broody hens. They took generally one-fifth of their normal intake and took more water than solid food. On some days they took no food at all. He fed to 2 cocks and 1 non-laying hen the equivalent amount taken by the hens. One cock died, as the broody hen whose diet he was having did not eat for three days. The broody hens lost 4-20 per cent. of their body weight while the 2 remaining controls lost 23-33 per cent.

Egg laying does not seem to be a pre-requisite to the onset of broodiness, for Pearl (1914) reports that several non-layers became broody, and one bird whose oviduct had been removed became broody. An autopsy, however, revealed that ovulation had occurred. Goodale (1916) induced brooding behaviour in 4 capons by presenting them with chicks. They were 2 Rhode Island Reds which are a broody breed, and 2 Brown Leghorns which are a non-broody breed. Although there were no great differences in the broodiness of the capons from the two breeds, one of the Rhode Island Red capons sometimes tried to tread his chicks. Pearl (1914) reports that the use of capons to brood chicks was a commercial practice in some areas. Goodale (1916) cites the case of a cock that hatched a clutch of eggs but this appears to be the only case published. Burrows & Byerly (1938) were able to induce broodiness in Rhode Island Red hens by placing them singly in a coop with baby chicks. The light was partly shut out to eliminate other visual stimuli. When the coops were replaced by darkened boxes with high temperature and humidity, broodiness was induced in two White Leghorn hens—a breed that is classified as non-broody. Furthermore broodiness was induced in a 12 week old crossbred pullet by these conditions.

Ramsay (1953) induced broodiness in 14 Cochin Bantam hens also by stimulating them with small chicks. He did not shut out other visual stimuli as Burrows & Byerly did, and so there was greater variability in the time taken for the birds to become broody. Generally he found that the more aggressive birds took longer to become broody. Burrows & Byerly (1938) found that better results were obtained when the birds were exposed to the stimulatory conditions in the afternoon rather than in the morning. All their Rhode Island Reds were broody within six days while 1 non-laying hen showed full expression in 18 hours, and 2 laying hens after one day. These results show that broodiness can be induced by visual and auditory stimuli.

Our knowledge of the physiological basis of broodiness in the chicken was taken a great deal further by the discovery of Riddle, Bates, and Lahr (1935) that broodiness in hens could be induced by injections of prolactin. Similar treatment caused Buff Cochin cocks to cluck. Burrows & Byerly (1936a) showed that single fowl pituitaries implanted over the crop glands of 8 ten week old pigeons caused prolactin-like reactions, and that the pituitaries from broody hens were far more effective than those of laying hens. Male pituitaries were approximately as efficacious as those of laying hens. They (1936b), showed by the same technique that the pituitaries of birds of broody constitution were more potent than those of birds from non-broody races. In their later work (1938) they found no difference in the effectiveness of the pituitaries of birds that had become broody through external stimuli, and those of laying birds. They therefore maintained that prolactin or some similar substance does cause broodiness under natural conditions but that it does not appear to be essential. However, until further work has been done this question must remain open.

Nalbandov, Hochhauser & Dugas (1945) produced broodiness in cocks by prolactin injections, and found that broodiness in males is due to the presence of certain environmental stimuli and to the absence of sex hormones. The prolactin inhibits the gonads by selectively shutting off the hypophyseal F.S.H. Nalbandov & Card (1945) were unable to get cocks to incubate eggs no matter how large the doses of prolactin. They therefore proposed that another hormone is necessary for this phase of the behaviour pattern. However until further evidence is forthcoming on this point, the explanation may equally be, that during the course of evolution the male has lost the necessary nervous mechanisms for incubating eggs.

Godfrey & Jaap (1950) were able to interrupt naturally occurring broodiness in 98 per cent. of 102 cases by a single 30 mgm. of oestrogen and from a small sample of hens the treatment did not appear to have an adverse effect on the resumption of laying compared with birds given the usual coop detention. They suggest that the oestrogen may act on the pituitary, not only to interrupt the production of F.S.H., but may also inhibit the production of other pituitary hormones including prolactin.

From the physiological viewpoint it is still uncertain whether the hormone occurring in naturally broody hens is really prolactin and whether a second hormone is also involved. It is also doubtful whether these hormones occur in hens that have become broody by external means.

This aspect of the reproductive drive undoubtedly has a genetical basis, for breeds differ a great deal in their susceptibility to become broody. (Pearl, 1914; Goodale, 1916; Nalbanov & Card, 1945; Riddle, Bates & Lahr, (1935). Goodale, Sanborn & White (1920) and Hays (1940) suggest that in Rhode Island Reds it is due to the presence of two complementary autosomal genes, while Kaufman (1948) using different breeds concluded that sex-linked genes and complementary autosomal factors are responsible.

Kuiper & Ubbels (1951) were interested in the temperature at which broody hens incubate their eggs. They found that the maximum temperature was 39.3°C., and that this occurred only where the egg was in contact with the hen. Irregular fluctuations occurred, especially when the hen left the nest, and when the eggs were turned, which was approximately once an hour. Since mortality is high during artificial incubation, further work on natural incubation would be valuable.

Summary

1. Broodiness may be interrupted by confining a hen to a detention coop.

2. It is cyclic in occurrence and may occur several times in any hen from March to June, but is not confined to one season.

3. The food intake of a broody hen is generally one-fifth of the usual amount consumed.

4. Egg laying does not seem to be necessary for the onset of broodiness.

5. Capons will readily brood chicks.

6. Broodiness can be induced in hens by visual and auditory stimuli, but more aggressive hens take longer to become broody.

7. Broodiness can also be induced by prolactin injections, and the pituitaries of broody hens, if implanted in the crop glands of 8-10 week old pigeons, cause prolactin-like reactions.

8. Cocks can also be made to brood chicks by prolactin treatment but not to sit on eggs.

9. Oestrogen injections can interrupt broodiness.

10. Some breeds differ significantly in their susceptibility to broodiness.

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STUDIES OF FIGHTING IN CHAFFINCHES

(1) BEHAVIOUR IN RELATION TO THE SOCIAL HIERARCHY

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For the purposes of this study, two flocks of captive Chaffinches were observed in successive winters, in a large aviary 9m. × 3m. × 2.5 m. They comprised four and eight birds, marked with coloured leg-rings, the sexes being equally represented in each flock. Observations were made from a hide at one end of the aviary, from the end of September to December. This paper thus deals only with fighting among Chaffinches in non-reproductive condition.

The Social Hierarchy at a Single Feeding Station

Two seed dishes were placed in the centre of the aviary, three feet above the ground. The results of fights that occurred during normal feeding behaviour are shown in Table I.

The Hierarchy at Various Feeding Stations

The hierarchy in one flock (8 birds) was examined at other feeding stations. The seed dishes were moved to the ground in the centre of the aviary, and then to one end. In each case the hierarchy was unchanged. Thus the outcome of fights between individual Chaffinches over food is independent of where they occur in the cage. During these experiments it was found that once the hierarchy was established, it remained more or less stable throughout the winter.

The Hierarchy in Fighting not Concerned with Food

In many of the studies of hierarchies in birds, attention has been concentrated on fighting arising during competition for food. It is of some interest to examine whether fighting in other contexts is in any way different, especially as the postures used are indistinguishable, both in wild and captive birds (Marler, In Press a). Records were kept of the results of all fights occurring on perches. These resulted either from competition for favourite perches, or from accidental proximity when birds alighted close together.

Table I. Records of the Victories by Birds on the Left of the Horizontal Rows over Birds in the Vertical Columns. (*a*) Flock one, records during thirty hours observation, 17.9.51—1.10.51. (*b*) Flock two, 10 hours observation, 8.10.52—15.10.52. All records are for encounters at food dishes in the centre of the aviary. Colour codes of males are underlined.

	B	O	W	Y
B	—	11	9	15
O	9	—	45	39
W	—	—	—	73
Y	—	—	—	—

(a)

	RWB	O	PW	RB	B	BW	R	Y
RWB	—	16	11	5	4	4	4	1
O	—	—	7	6	16	4	4	6
PW	—	—	—	4	7	10	10	3
RB	—	—	—	—	12	13	8	8
B	—	—	—	—	—	3	8	5
BW	—	—	—	—	—	—	5	2
R	—	—	—	—	—	—	—	11
GY	—	—	—	—	—	—	—	—

(b)

It is clear that in fighting at this particular feeding station both flocks were organised in a peck-right hierarchy, of the simplest straight-line type. The despot or alpha bird won all fights, the omega bird none. The apparent irregularity in flock one resulted from a reversal of dominance between Male O and male B partway through the experiment. As in the wild state (Marler, In Press a) males were dominant over females.

The results of these fights revealed straight-line hierarchies identical with those concerned with food. The number of such fights recorded (c. 240 for each flock) was rather greater than the number of fights over food (c. 200 for each flock).

Diurnal Variation of Fighting at Seed Dishes and Perches

Fighting is most common at certain times of day. If fighting over food and over perches differ, the two types might not fluctuate in the same way through the day. The observations on the flock of four birds were divided equally among three sectors of the day 0900—1100 h., 1100—1400 h., 1400—1700 h., The average frequencies were 7.8, 5.8, 6.6, encounters per hour for food fighting, 10.1, 6.3, 7.6, for perch fighting. Fighting in both contexts was thus most common in the morning and rarest in the middle of the day.

Diurnal Variation of Other Activities

In an attempt to link up the variation of fighting with other activities, records were kept of the behaviour of the flock of four birds at five minute intervals. They were classified as perching (sitting still), preening (always on a perch), foraging (on the grass floor of the aviary), feeding (at the seed dishes), drinking or bathing. Because of the difficulty of identifying birds in flight, the activity performed on alighting was recorded. In general, restless movement appeared to vary inversely with preening. Table II is derived from about a thousand records, reduced to percentages.

Both preening and feeding are somewhat more common in the evening. Rather more of the time spent perching is used for preening than at other times. The sum of perching and preening increases in frequency through the day. This seems to be linked with the converse change in foraging, which varies independently from feeding at the dish.

The Relationship Between Hierarchy Status and Certain Activities

From the same data, the diurnal variation of the activities performed by each of the flock members have been calculated (Table III). The figures are so reduced that the differences are barely significant, but certain trends can be detected.

It is clear that while all birds were involved in the increase of preening and the decline of foraging during the day, the increase of feeding can be mainly attributed to the two lowest ranking birds. The other two feed at the same rate throughout the day. Thus we are no nearer to understanding the variation in fighting. But there is nothing to suggest that fighting on perches and over food are different phenomena.

Feeding behaviour was also studied more closely by recording the time spent feeding by all four birds. The average number of visits per hour, during 30 hours of observation spread evenly over the day for several weeks, was B—2.3, O—4.4, W—5.3, Y—5.1. Thus the low-ranking birds visited the food dish more often than those of high rank. This is to be expected since subordinates are continually displaced from the food by dominants. The average duration of visits to the food decreases down the hierarchy, B—3.2 mins., O—2.01 mins., W—1.64 mins., Y—1.29 mins. Thus subordinates make a greater number of shorter visits than dominants. By combining these figures we derive the time per hour spent feeding, B—7.36 mins., O—8.85 mins., W—8.69 mins., Y—6.58 mins.

Table II. The Frequency of Various Activities in a Flock of Four Birds, during Three Sectors of the Day, Expressed as Percentages

	0900—1100 h.	1100—1400 h.	1400—1700 h.
Perching	55·9	60·4	53·7
Preening	14·8	14·5	23·8
Feeding	12·1	13·6	16·4
Foraging	16·7	11·1	4·6
Drinking	0·54	0·32	1·2
Bathing	0	0	0·31

Unexpectedly, no activity varied directly or inversely with fighting, except perching, which was slightly but probably insignificantly more common at midday, and drinking which was slightly but insignificantly less common. In particular fighting over food does not necessarily link up with time spent feeding, nor over perches, with time spent perching.

Table III. The Frequency of Certain Activities, Converted to Percentages, of Individual Members of the Hierarchy during Three Sectors of the Day, 0900—1100 h. (1), 1100—1400 h. (2), 1400—1700 h. (3). B is the alpha, Y the omega bird

	B			O			W			Y		
	1	2	3	1	2	3	1	2	3	1	2	3
Sitting	59	66	48	43	43	54	60	56	44	61	77	68
Preening	17	13	35	16	19	20	14	19	27	12	8	14
Feeding	10	11	12	16	17	15	13	15	22	10	11	16
Foraging	14	10	4	24	20	9	12	10	4	17	4	2
Drinking	—	—	1	1	1	2	1	—	1	—	—	—
Bathing	—	—	—	—	—	—	—	—	1	—	—	—

Although as expected, the omega bird is unable to spend as much time feeding as the others, it is remarkable that the despot, which is free to feed at any time it wishes, seems to feed less than the two middle birds. This may be a result of learning to take as much as they can, as a result of previous deprivation by the despot (cf. Hebb, 1949).

The Relationship between Hierarchy Status, and Aggressive Behaviour and General Deportment

The aggressive displays used during fighting in winter (see Marler, In Press a) were most intense and prolonged between combatants close in rank. In these and other experiments it was found that inversions of dominance were accompanied by the fiercest fighting of all. High-ranking birds would make direct supplanting attacks on low-ranking birds, without any preliminary display. Males often attacked females more confidently than other males. Some birds showed submissive behaviour (Marler, loc. cit.) which prevented others from attacking them. This was usually only seen from females, generally only from the omega female while in contact with the despot.

In these and other experiments, it was sometimes possible to see general differences in the deportment, while not fighting, of birds of various ranks (Hinde, 1953), especially when crowded in small aviaries. The despot could usually be identified by his alert behaviour involving free movement and visual examination of the environment. In particular the movements of pivoting and tail-flipping (Marler, In Press a) were freely used, in contrast with the other birds. They also used the alert posture, but rather tensely, and movement was especially restrained when close to the despot.

The Effects on Fighting of Increased Competition for Food

Members of an established flock know that they can attack subordinates freely, but flee promptly from dominants. Because of the small size of the seed dishes provided, generally only one bird fed at a time. They would usually avoid approaching a dish already occupied by a dominant bird. If they approached they were repelled, unless they managed to inhibit the dominant's attack by submissive behaviour. It might be expected that the proportion of approaches made by dominant birds to a dish occupied by a subordinate, to the approaches of subordinates to a feeding dominant (d/s) would be reduced as competition for food was increased. By comparing the ratios in small and large aviaries with different numbers of birds (Table IV) this was found to be generally true.

By dividing the results for each flock into approaches of males to males, females to females, and females to males, it was found that females tended to approach feeding dominants of either sex more often than males approached their own sex (Table IV).

Effects of this kind might be due to changes in either the dominant or the submissive bird. However there is strong evidence that increased competition has no effect on the aggressiveness of dominant birds (Marler, In Press c). The results can therefore be explained by variations in the tendency of subordinates to avoid a dominant.

The Effects of Starvation on Fighting

Another method of increasing competition is to starve birds and then provide them with a limited source of food. Several such experiments were conducted in a 6′ cube aviary with a single

Table IV. Ratio of Dominant Approaches to Occupied Food: Subordinate Approaches (d/s). A high value thus indicates that subordinates avoid approaching food where dominants are in possession. In the mixed flocks the encounters have been separated into male-male, female-female and male-female contacts

	d/s males	d/s females	d/s males/females
Large aviary, two males, two females	20	—	8·3
Four males, four females	4·6	9·3	3·6
Small aviary, eight males	5·6	—	—
Eight females	—	3·4	—
Four females and four males	2·7	0·09	0·76

seed dish, flocks of eight birds being starved for periods up to two hours (Table V).

The effect on a male flock was to increase the number of subordinate approaches to feeding dominants until they roughly equalled dominant approaches (with a d/s ratio around 1.0). With a flock of eight females the effect was similar but the ratio of d/s began smaller, and fell rather below 1.0. In a mixed flock it never rose above 0.8, and fell as low as 0.3. Here there were on occasions more than three times as many subordinate as dominant approaches. Thus passing from male, to female, to mixed flocks, the fear that subordinates had of dominants was found to be progressively less.

The meaning of these differences is made clearer by considering how the increasing numbers of subordinate approaches are received by dominants. It has been pointed out that a subordinate which approaches a feeding dominant may either be repelled from the dish, or may be tolerated if it shows submissive behaviour. Table VI shows the proportion of subordinate approaches to feeding dominants resulting in toleration (t/s) in three flocks, after various periods of starvation.

Considering the flocks of one sex first, in the males, subordinate approaches after starvation were usually greeted with aggression, as under normal conditions, and hardly ever with toleration. In the female flock on the other hand, the majority were greeted with toleration.

Table V. The Effects of Short Periods of Starvation on the Ratio of Dominant Approaches to Occupied Food; Subordinate Approaches (d/s) in Three Flocks

	Minutes of Starvation						
	0	15	30	45	60	90	120
d/s : Eight males	10·4	2·1	5·5	0·73	1·6	0·8	1·3
d/s : Eight females	3·9	2·3	1·4	0·55	0·80	0·75	0·97
d/s : Four males and four females	0·79	0·74	0·63	0·49	0·66	0·29	

Table VI. The Proportion of Subordinate Approaches (s) to Feeding Dominants, that Result in Toleration (t) by Dominants, Expressed as the Ratio t/s. Thus a ratio of 1·0 implies complete toleration, a ratio of 0, no toleration at all

	Minutes of Starvation						
	0	15	30	45	60	90	120
t/s Eight Males	0·43	0·57	0·05	0·06	0·09	0	0·12
t/s Eight females	0·54	0·66	0·77	0·90	0·84	0·82	0·79
t/s Four males and four females	0·90	0·89	0·82	0·58	0·65	0·64	—

Thus although under normal conditions the subordinate birds in both male and female flocks normally avoided dominants, and were usually repelled if they approached (Tables IV, V, VI), after starvation females tolerated each other. It might be inferred from the results that dominant males were actually more aggressive to subordinates after starvation (Table VI). But this effect only appears because under normal conditions males usually only approached dominants when they were sure of being tolerated, whereas after starvation they would approach all dominants indiscriminately.

Since aggressiveness as such is not affected by starvation, these results imply that dominant females are more tolerant of subordinates whose fear has been reduced by competition or starvation. In other words they are most ready to attack a subordinate which shows a tendency to avoid them. This is of course a phenomenon observed in the normal fighting behaviour of many species (Schjelderup-Ebbe, 1935; Marler, In Press a). Although very aggressive birds will attack an opponent however it behaves, more timid ones wait for definite signs of fear before attacking. It appears that male Chaffinches come into the first category and females into the second. And in females the balance is sufficiently delicate that even if a dominant has learned to attack subordinates under normal conditions, a reductions in their fear causes the attack tendency to disappear.

The effects of starvation on the mixed flock were intermediate between those on male and female flocks, (Table VI). There was more toleration of subordinates than among males, but less than among females. This was partly a result of averaging out between aggressiveness among males in the mixed flock, and toleration among the females, but this would lead to much lower ratios of t/s than were discovered. This was corrected by the males, which are more tolerant of females under normal conditions (page 113), and continued to tolerate them after starvation.

Thus it appears that while males continued to attack subordinate males whose fear has been reduced by starvation, they would tolerate subordinate females under the same conditions. This suggests a different response to the morphological characteristics of males and females, as further experiments, using females disguised as males, have substantiated, (Marler, In Press b).

Discussion

(*a*) The social hierarchy. As in many species (Schjelderup-Ebbe, 1935; Collias, 1944; Allee, 1950) the outcome of fights between Chaffinches which know each other is more or less predictable. The one assured of victory is said to be dominant, the victim subordinate.

The two main types of social hierarchy may be described in terms of the parameters that must be taken into account, for accurate prediction. In a "peck-right" hierarchy (Schjelderup-Ebbe, 1922) it is sufficient to identify the individuals concerned, but in a "peck-dominance" (Masure & Allee, 1934 a, b) hierarchy it appears that the location of the fight must also be considered (Diebschlag, 1941; Ritchey, 1951). The latter seems to correspond to the territorial behaviour of Passerines, but on a smaller scale (Allee, 1942, 1950). A bird is dominant within its territory, and subordinate outside it. Both types of hierarchy may occur among Chaffinches, "peck-right" in winter, "peck-dominance" or "territorial" during the breeding season (Marler, In Press a).

When "peck-dominance" hierarchies were first described, the importance of territory was not realised. The outcome of fights was predicted in statistical terms, hence the use of the term "dominance." As a result it has sometimes been applied subsequently to individuals which are evenly matched (e.g., Sabine, 1949). But in fact a state of dominance cannot be said to exist in such cases, since the results of fights are not predictable.

It has been shown that hierarchies also occur among wild birds. "Peck-right" hierarchies have been described at single feeding stations in winter flocks of Black-capped Chickadees (Odum, 1942, Hamerstrom, 1942), Blue Tits (Colquhoun, 1942) and Great Tits (Brian, 1949), Juncos and Tree Sparrows (Sabine, 1949). However it is possible to obtain an apparent "peck-right" relationship in a society that is actually organised in a "peck-dominance," by recording encounters at one station (Ritchey, 1951). "Peck-right" cannot therefore be regarded as proved in the wild state until observations are made at more than one station. The fact that a relationship between distance of the feeding station from the summer territory, and status in the hierarchy, was found in all the Paridae quoted above, might rather suggest "peck-dominance" relationships.

(*b*) Fighting in various contexts. The results of fights among Chaffinches over both food and

perches are the same. The postures used are similar, and both fluctuate through the day in the same way. Both seem to vary independently of the other activities recorded, including feeding and perching. Thus all the evidence suggests that they are similar phenomena.

In the field (Marler, In Press a) fighting usually occurred because a bird, for some reason came too close to another. When a certain distance around each bird, the "individual" distance (Hediger, 1950), was violated, signs of aggression always appeared. The same conclusion may be applied to fighting in aviaries. Thus food and perches may be involved in fighting, only as the factors causing proximity. By experimental study it was found subsequently that this "individual" distance is readily measured and the view is taken that its violation is the basic stimulus for aggression (Marler, In Press c).

(*c*) Differences between male and female fighting. Male Chaffinches dominate females, and in general appears more aggressive. However they are more tolerant of females than of other males. This is at least in part an effect of male colouration (Marler, In Press b, c), for females, artificially coloured like males, are tolerated less readily than normal females. Females are also less ready than males to attack subordinates of their own sex, especially if their avoidance tendency has been reduced by starvation. This may be taken as another aspect of their weaker aggressiveness, for the same phenomenon may be observed among hens (Schjelderup-Ebbe, 1935). A strongly aggressive hen will attack others however they behave. A less aggressive one waits until its opponent shows signs of fleeing, before pressing an attack home.

(*d*) The effects of starvation on behaviour. The effect of starvation is to increase the tendency of birds to approach a seed dish, whether or not it is already occupied by a dominant bird. There were also suggestions that avoidance responses in other contexts were reduced. Starved birds showed less agitation than usual, on the approach of a human observer. This was most apparent in low-ranking birds, which would normally be short of food. Even under normal aviary conditions, some subordinates developed the habit of taking the chance to feed during disturbances, while the rest of the flock showed escape behaviour.

Thus it appears that starvation reduces responses to escape stimuli in general, not merely those emanating from a food source. This has been clearly demonstrated in mammals. Hall (1935, 41) found that hungry rats are less timid in strange surroundings than satiated individuals, and concluded that "needs other than the need to escape, inhibit the display of emotional behaviour, by distracting the animal from the fear-provoking aspects of the situation." This explanation may well apply also to the Chaffinch.

Summary

Two captive flocks of Chaffinches were organised in straight-line, peck-right hierarchies with males dominant over females, the results of fights being the same wherever they occurred in the aviary. Fights over food and over perches had similar results, and varied in frequency through the day in the same way. The diurnal variation could not be linked with that of other activities, including feeding and perching. All fighting appeared to be caused by one bird coming too close to another.

In a flock of four birds, the two of low rank made shorter and more frequent visits to the food dish than the others. The two middle-ranking birds spent more time feeding than both the alpha and omega birds. Behaviour during fighting and at other times varied with rank.

Experiments on the effects of starvation on fighting showed that males were more tolerant of females than of each other. A female would not press an attack home against another female until it showed signs of fleeing, but a male would attack another male however it behaved. Starvation reduced the tendency of subordinates to avoid dominant birds, and probably also avoidance responses to environmental stimuli.

The nomenclature of hierarchies is discussed, and the evidence for the existence of peck-right hierarchies in wild flocks is questioned.

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OLFACTORY MARKING OF TERRITORY IN TWO YOUNG MALE LORIS, *Loris tardigradus lydekkerianus*, KEPT IN CAPTIVITY IN POONA

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With four photos by K. Raschke, Poona.

Two very young males of *Loris tardigradus* were purchased in Bangalore in June, 1954, and taken to Poona where they have since been observed. For the first few weeks, they were unable to eat solid food and had, therefore, to be bottle fed on cow's milk. After that, they accepted insects as additional food and are now taking living insects and lizards apart from drinking buffalo's milk out of a dish. They are allowed to roam freely in a room of 200 by 370 cm. in my bungalow in Poona. They have not become diurnal (as reported for some Lorisids by Pocock 1939). The reason for their adherence to nocturnal life may be that their room is provided with a device (a weak electric bulb inside an organtin cube) which lighted all, or almost all, of the night, attracts many insects from outside, on which they feed. Their exact ages are not known, but are roughly estimated to be (January, 1955) nine and eleven months respectively, the smaller one not yet having reached full size. I have been able to confirm many observations published by previous authors, for example, their food preferences, their inability to leap, their tendency to stay in a high place and to avoid coming down to the floor, (Pocock 1939). I have also seen some responses which to my knowledge have not hitherto been mentioned, among these certain "convulsive" movements occurring in their mutual or solitary play (c.f. Chance, 1953). While many of their habitual movements appear rather flexible, I shall now describe two of their more stereotyped behaviour patterns, both of which are connected with micturition.

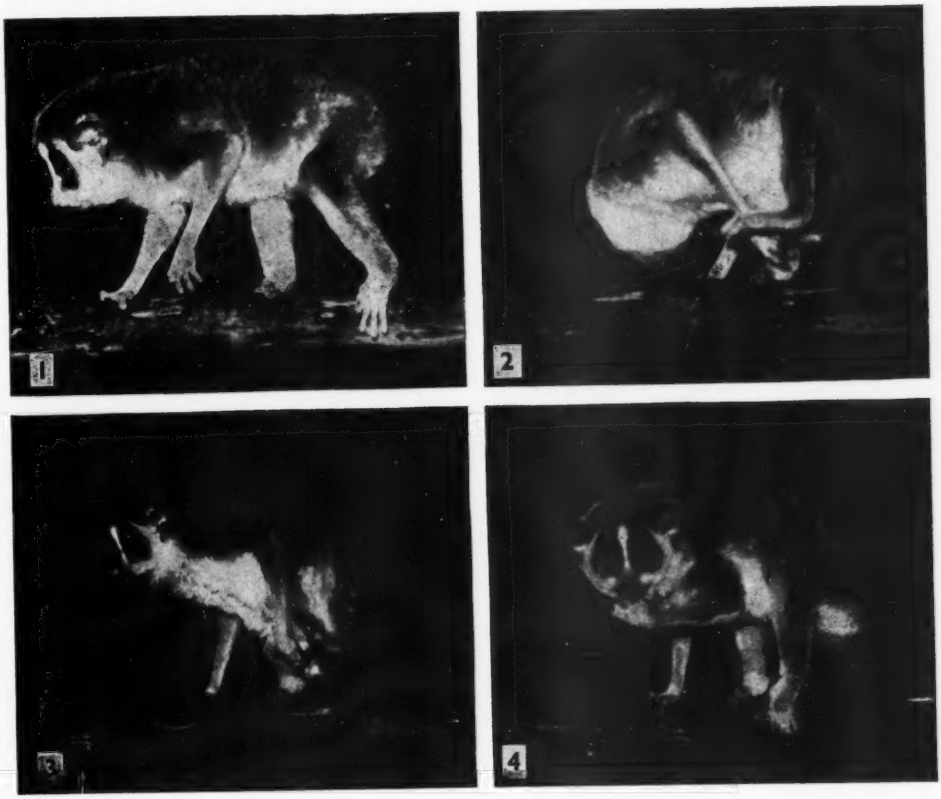
The room allotted to the young loris contains among other items, sideboards, some glass cages containing other animals, a ladder, a swing, and a great number of strings and ropes fixed at one or both ends, which enable travel from one spot to the other and along the ceiling. During the night when they are active (from about 8 p.m. to 7 a.m.) I can observe them through an opening in the door of the adjacent room, but they do not seem to mind my presence in their room, where from time to time they take food out of my hand or come running to sit on my shoulder (this applies mainly to the smaller loris who was brought up by myself alone). Conspicuous among the objects in the room is a long pole connecting the right with the left wall, which they use as a part of their "beat" when running from the swing or some place under the ceiling, to their "nest," or to some other favoured spot. When they are running over this horizontal pole, using all four legs, the very flexible spinal column is usually carried parallel to the pole, i.e., horizontally, or nearly so. (see Fig. I) When the loris encounters some strange object, it lowers its head together with the anterior part of his body in order to sniff at it.

It was not until August, 1954, that quite a different type of movement, involving a different carriage of limbs and body, was observed.

Rhythmic Micturition

The loris begins to walk at one end of the horizontal pole described above, lowering his hind body and at the same time sprawling his hind legs so that he takes up a "crouching" position during which one leg may, or may not, hang down freely from one side of the pole, He then proceeds walking further along the pole, dragging his hind part along its surface which, however, may be raised and lowered rhythmically in the course of the walk so that some kind of undulating movement of the spine results, which sometimes gives an impression of curtsying. Every time his hind part touches the pole, the loris will pass a few drops of urine, part of which naturally flows down the pole so that by the time he has reached the other end the whole length of the pole will be sprinkled over with urine, while at the same time a parallel row of urine drops can be seen on the store floor underneath. Often when direct observation during the night has been impossible it was the presence of such a row of drops discovered on the floor which indicated to us that such a rhythmic micturition must have taken place. A loris walking over the pole in such a fashion, may occasionally sniff at it, removing some bit

PLATE I



of bark from its surface which had previously been wetted either by its own urine or that of the other loris, to chew at it for some time. It is suggestive that the pole would thus be marked by the male animal with his urine, in order to be claimed by him as a personal track or beat, connecting important places situated within his territory (Hediger, 1950).

Micturition may also occur on sideboards, tops of glass cages, and other horizontal surfaces, but in these places it has not been observed by us to be desposited in a rhythmic fashion. Those sites may rather be considered to be "urinals" (Hediger); layers of cotton wool, placed there, often seem to act as an additional stimulus eliciting micturition. On the other hand the pole, having very little surface to sit on, can hardly be a satisfactory urinal, nor provide a surface of such alluring smoothness. Above all, the fact that the urine is here deliberately distributed, in small drops, over the whole length of the accessible surface of the pole, seems to indicate that this is rather a special form of micturition, different from the usual type as observed in other places. This form, therefore, has been interpreted here as part of an "olfactory marking of territory."

Urine Washing

These observations suggest that another fairly stereotyped behaviour pattern connected with micturition, which has been described before for Lorisids and related animals, might rightly be interpreted as a second, complementary method of such olfactory marking of territory. This is the so-called urine-washing habit, already described by some authors (Pocock, 1939; Boulenger, 1936) for the African Galagos, and by Osman Hill for Lorisids and platyrrhine monkeys alike. However, the description of the habit by these authors differs slightly from mine regarding certain details of movement; no pictures seem to be available; and there has been some controversy as to its interpretation.

Each of our two loris showed this behaviour in various positions, such as hanging from rope, sitting on his haunches while leaning against some support, but preferably again, when running over the above-mentioned horizontal pole. Invariably, it has been observed here to occur in the following way. The loris, standing on the pole on all fours lifts his left hand and left foot together so that he now stands on his right hand and right foot alone perfectly balanced. In this, he is helped by a curvature of the spine which may sometimes attain a semicircle (see Fig. 2), and occasionally, he is supported by his hind end touching the pole slightly. Immediately, the following phases are executed at such speed that detailed observation is difficult. The left foot moves backwards towards the genital area, with the sole and inside of the outstretched digits pointing forward, downward, and very slightly outward as in walking, while the thumb (hallux) is stretched inward forming approximately a right angle with the rest of the foot. It is peculiar that in this position, the dorsal side of the tip of the hallux, not the ventral side as one might expect, touches the genital region to exert a slight pressure. Simultaneously, the left hand has been moved backward first, behind the foot, (see Fig. 2) then forward again, so as to form a cup held in front of the hallux. Apparently due to pressure applied by the dorsal side of the hallux, a drop of urine or two are then squeezed out which are immediately caught in the cupped palm of the left hand (Fig. 3). At once the left foot moves away from its position to forward and outward from the genital region, (following the movement of the whole leg), while the left hand follows the movement of the left foot until its palm lies flat on the sole of the latter, when a vigorous rubbing of these two against each other is started which is often helped by rotating, or even sometimes clapping movements of both hands and foot. In this way, the urine that had been collected in the cupped left hand, is being distributed all over the left palm as well as over the sole and the inside of the digits of the left foot. While it is not often possible to see actual drops of urine, except in the first stage when occasionally a few may fall on the floor, the glistening of the left palm and sole with moisture can always be perceived quite distinctly during and after the wiping process. The whole procedure here described, measured with the stop watch, was found to take not more than two seconds. Afterwards, the loris occasionally may lick the hand used for collecting the urine (see Fig. 4), but in most cases the whole pattern of behaviour is immediately repeated with both hands and foot of the other side. This alternating washing of right foot with right hand, and left foot with left hand, may go on for some time. I have never seen a foot washed by the hand of the opposite side, or one hand washed by the opposite hand, as described by Hill (1953). The sequence of this movement when performed on a horizontal

surface—as it usually is—appears rather stereotyped, though there may be slight modifications if and when it is performed in unusual situations, e.g., by animals hanging down from a rope.

The fact that this particular behaviour pattern is often followed immediately by that of rhythmic micturition, as described above, has suggested to me that this washing with urine may be an additional method for marking the territory. While rhythmic micturition by its nature can be effective only on horizontal surfaces and not on more or less vertical ones like branches of trees, the hands and feet smeared over with the individual urine of any male in this process of urine-washing must leave a scent track even on such vertical surfaces that can be smelt by other male (and perhaps female?) loris. One feels tempted to suggest that some secretion from a scent gland, may be squeezed out by the hallux at the same time as the drops of urine, particularly since Hediger has mentioned (1954) that some Lemurs are provided with stink glands. However, I have not been able to verify whether any such glands are present in the genital region of *Loris tardigradus*.

This interpretation of the urine washing as additional olfactory marking of territory, by no means excludes or contradicts another interpretation, given by most earlier authors, of its having the effect of making hands and feet smooth for climbing (Hill 1938). In fact, it might well serve both purposes. As for its occurrence in an emotional state, as claimed by Hill, this I have not been able to confirm; my loris react to emotional situations either with "convulsive" play movements, or by producing chattering and growling noises. It is, however, conceivable that in such states, under certain circumstances, the urine washing may have been performed as a displacement reaction. It will be important to observe the behaviour of female loris in similar situations.

The fact that in the cases described here, both urine washing and the rhythmic micturition, have been observed in young immature loris, raises the question of the age at which such responses will develop, and what is their exact function under normal conditions of jungle life. During the period of observation, my loris were from three to about eleven months old, an age at which, according to Shortridge (quoted by Pocock, 1936) they are normally still suckled by their mothers. Supposing our interpretation is correct, we may wonder whether these two motherless babies have developed prematurely what is normally an adult behaviour pattern, or whether the young male loris may even in the wild state, start at an early age to help with the marking of his parents' territory. It may be noted that each of our two immature loris used to mark the *same* preferred places within their small territory, apparently singling out a place which had already been marked by the other. This behaviour used to go hand in hand with a more or less good-natured battle for dominance, observed with regard to food grabbing, mutual grooming, and choosing of favourite resting places. Such fighting has only quite recently become so ferocious that the two males had to be separated: a fact which seems to bear out Shortridge's statement that "their quarrelsomeness when kept together in a cage shows that they are not naturally gregarious." Further observations should show what effect the isolation of the lorises will have on their different "marking" patterns. Thus far, the small male's activities appear to be generally restricted after the separation from what had become his enemy.

Summary

Two types of stereotyped behaviour involving micturition, have been observed in two immature males of *Loris tardigradus* from Bangalore, kept in captivity in a room in Poona. They are "rhythmic micturition" and "urine washing" respectively, and are provisionally interpreted as "olfactory marking of territory."

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This paper is dedicated to Professor A. Kühn, Tübingen, on the occasion of his 70th birthday.

PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

At an Ordinary Meeting of the Association held in the Department of Psychology, Birkbeck. Malet Street, London, W.C. 1., on Thursday, 28th of April, 1955, the following papers were read, The subject of the meeting was "Imprinting" and the President, Dr. A. Walton, was in the chair.

THE NATURE AND SIGNIFICANCE OF IMPRINTING

By W. H. THORPE

Zoological Laboratory, University of Cambridge

Imprinting, probably should not be thought of as a distinct type of learning. But it is nevertheless of exceptional interest in its extreme manifestations, as a very rapid, unrewarded perceptual learning strictly limited both in time and direction. Its function seems to be to build rapidly upon and so complete the adjustment of the Innate Releasive Mechanisms of certain social behaviour patterns which are of crucial importance in the life history of the organism. The principal characteristics are as follows: (1) The process is confined to a very definite and brief period of the individual life, and possibly also to a particular set of environmental circumstances. (2) Once accomplished it is often very stable—in rare instances perhaps totally irreversible. (3) It is often completed long before the various specific reactions to which the imprinted pattern will ultimately become linked are established. In such cases it is (4) supra-individual learning—a learning of the broad characteristics of the *species*—for if this were not so and the animal at this stage learnt (as it can easily do later) the individual characteristics of its companion, the biological effect would be frustrated.

A brief survey of the incidence of imprinting in the animal kingdom was given followed by a critical comment on some of the more important experimental studies on the subject. It was pointed out that in very few of such studies has the factor of secondary reinforcement been adequately controlled.

THE FOLLOWING RESPONSE OF MOORHENS AND COOTS

By R. A. HINDE

(Based on work carried out in collaboration with Dr. W. H. Thorpe, F.R.S., and Miss M. A. Vince)

Ornithological Field Station, Madingley; *Cambridge University Department of Zoology*

This paper was concerned with the preliminary results of an investigation of the factors controlling the following response of young Moorhens (*Gallinula chloropus*) and Coots (*Fulica atra*). The birds were reared by hand under infra-red brooding lamps, and tested in an outside grassy pen 24 yards long by 6½ yards wide. Models could be moved along a wire in the middle of the pen. In most cases each individual was given three runs a day. The following conclusions can be drawn from the results so far obtained:

(1) The following response could be released by a number of objects quite different from each other in size, shape and colour, but having in common the character of being in motion.

(2) The establishment of the following response to any particular object was not dependent on that object being associated with brooding, feeding or any other activity normally directed by the parent to its young.

(3) Birds were more likely to follow models if tested from the first day after hatching than if testing was delayed for a few days. In the latter case most birds fled from the model. This increasing tendency to flee is probably the most important factor in limiting the period during which a following response can be established in these species ("the sensitive period").

(4) Birds could be trained to follow different models on successive runs (e.g., a wooden model of a moorhen, a black wooden box 12″ × 8″ × 5″, and a large khaki canvas hide 5′ × 3′ × 2′, each shown once a day). Further, birds trained on one or a few models would generalize to

other models throughout practically the whole period in which they would follow at all: new models were followed most strongly by those individuals which had previously followed the regular models well. (Generalization was, however, followed by interesting changes in response strength which require further study).

(5) Following was maintained under conditions of massed practice (one run per minute) with greater stability when the object to be followed was a familiar one. With an unfamiliar object there was usually a progressive decrease in the response, which was sometimes followed later by a recovery. This suggests that persistent following is given only to a familiar model—and that the stimuli to which the animal learns to respond not only elicit the response, but also have a reinforcing effect (Hinde, 1955. *Adv. Sci.* **45**).

Lorenz (e.g. 1937. *J. Orn.*, **83**, 137-213, 289-413) regarded "imprinting" as a distinct form of learning by virtue of four characteristics: the first two of these were that the learning is confined to a definite and short period of the life cycle, and that it is irreversible. Our results show that in Moorhens and Coots the learning is not irreversible. They also suggest that the "sensitive period" is not a property of the imprinting but a consequence of the increasing strength of the fleeing response. The third and fourth of Lorenz's characteristics refer to the subsequent direction of the animal's sexual responses towards objects similar to those on which it had been "imprinted" as a juvenile. We were not able to test for such effects in Moorhens and Coots because they became too wild, but such effects can hardly be used as *characteristics* of the initial process of learning to follow a "parent"-object, though they may be *consequences* of it. The learning processes involved in the establishment of this response thus show no absolute differences from other cases of associative learning (cf. Fabricius, E. (1951) *Acta. Zool. Finn.*, **68**).

EXPERIMENTS ON THE FOLLOWING-RESPONSE OF MALLARD DUCKLINGS

By ERIC FABRICIUS

Institute of Fresh-Water Research, Drottningholm, Sweden

The paper is a report on a joint work by Hugh Boyd (The Wildfowl Trust, Slimbridge) and the author.

Mallard ducklings, hatched in incubators, were confronted with simple models in a runway. Most of the models used were boxes or balloons which could be pulled in either direction. The birds reacted to them by following, aggression or avoidance. Any model could elicit all these responses.

The sensitive period of following was not very sharply limited, but the highest proportion of followers was found in ducklings of 25-50 hours. Older birds tended to show initial avoidance rather than following. Ducklings failing to follow the models, also tended to avoid other ducklings on first meeting them.

In some experiments the birds in one group were shown a balloon at first showing, whereas those in another group were shown a box. At subsequent showings after intervals of two days or more, some were given the "strange" model, others the "familiar" one, and others a choice. While several followed the strange model in addition to the familiar one, in all cases the response to the former was less intense. Some model-followers developed a tendency to follow men after some weeks.

A NOTE ON THE SELECTION OF LOVE OBJECTS IN MAN

By JOHN BOWLBY

The Tavistock Clinic, London

Many clinical problems (e.g., ambivalence to love object, inability to love, fetishism and homosexuality) are disturbances either in the selection of the object or in the organisation of impulses directed towards it. Clinicians are mostly concerned with the development of relations with a particular object and not, as in imprinting, with relations to a class of objects. Nothing is known of imprinting in man.

Two theories are current about the nature of the infant's first relationship to the mother—(i) that the infant has no innate interest in humans but learns to be interested in them because they satisfy primary physiological needs, (ii) that his social interests and needs are

themselves as primary as his physiological needs.

In the period three to seven months the infant learns to discriminate his mother from others and thenceforward becomes attached to her as an individual: an intense need for attachment continues until after three years and appears similar to the following response of other mammals. Clinical experience suggests that the phases during which differentiation takes place and during which the following response is at a maximum are critical for the development of the child's relation to his parents and also for his adult social responses, such as the sexual and the parental.

AN HYPOTHESIS ON IMPRINTING

By W. S. VERPLANK

Harvard University

The hypothesis presented is a development of that set forth by William James, in his *Principles of Psychology*. Sketched out by James, it can now be more fully developed, thanks to half a century of research on learning. The general principles very likely account for most of the importance of early experience to phenotypical behaviour.

Imprinting is regarded as simple stimulus-response learning occurring under somewhat special conditions. An initial weak tendency to follow moving objects of specifiable size is strengthened by repetition of the following behaviour. This following behaviour becomes restricted to a specific class of object by a later-appearing species-specific tendency to fear and to escape from objects of the same general class as that which initially excited following. Only the class of objects that the animal has had extensive practice in following retains the property of exciting following; the animal remains "tame" with respect to it. This sparing is a case of the transfer phenomenon called proactive inhibition in other contexts.

When adult behaviours appear, proactive inhibition should lead to interference (by persisting fear and flight components of behaviour) with response to those objects that had *not* been followed prior to the appearance of the fear and flight behaviour in the animal's early days.

The hypothesis is consistent with data that have appeared in the literature, and provides a basis for interpreting it. It also suggests that further experiments will reveal specific relationships between the strength of following behaviour in the young animal, and the strength of imprinting observable in the adult. It suggests analyses of the complex and apparently conflictful components of courtship and mating.

According to it, imprinting, as it has been found (and studied intensively) in some species of birds should be found in all social species whose young can walk or swim shortly after birth or hatching; and that it should not be clearly evident in those species whose young are not capable of locomotion through their first weeks or months of life.

THE DOUBLE RELEVANCE OF IMPRINTING TO TAXONOMY

By H. SPURWAY

Department of Biometry, University College, London

Imprinting is a process of learning to react to categories, not individuals. It does not depend on reinforcement.

Imprinting is therefore important to taxonomy: firstly because the human capacities for this process are relevant to our recognition of categories, and secondly because non-human species' capacities for recognising categories play a part in the establishment of the reproductive isolation of populations.

There are resemblances between imprinting and intuitive taxonomy (cf. Pantin, *Sci. Progr.*, **42**). The only difference between these processes is that members of *Homo sapiens* do not lose their infantile capacities abruptly.

The *species* and comparable words describe those categories to which human beings are capable of being imprinted. Whether these naïve species correspond to reproductively isolated groups of populations depends on whether human beings have been ecologically related to the non-human organisms long enough to have *evolved* the nervous mechanisms capable of the relevant *developmental* processes. Non-

human species' capacities for non-reinforced learning are relevant to understanding the disturbances of taxonomy consequent on both modern techniques (e.g., cytology) and modern concepts (e.g., evolution theory).

The species seems less arbitrary than other taxonomic categories not because it "can be defined biologically" but because it is recognised by capacities which are prehuman and prelinguistic. It can be recognised "biologically" and for that reason, is heterogeneous and therefore indefinable. Subspecific and supraspecific categories are constructs of human language. Language structure itself and other human artifacts are dependent on imprinting.

Many of these arguments are in press in *J. Genet.*, **53**, and *Proc. XI Ornith. Cong., Basel*, 1954.

CORRIGENDUM

Vol. III, p. 74. N. Moore is the author of the abstract, "A Behaviour Study of Dragonfly Numbers," which appears on this page.

Just Published

Psychology and Behaviour of Captive Animals in Zoos and Circuses

By Dr. H. HEDIGER

Director of the Zoological Gardens, Zurich

The points of similarity in the behaviour of the animals on both sides of the zoo railings become too obvious to miss. We see much in the behaviour of an animal that is human—all too human—and often regard as animal some of the actions of man. That is the point of view from which this book has been written. The author regards animal psychology, as a branch of human psychology, indeed of psychology itself, though he deplores the greatest danger in trying to understand an animal—the tendency to humanize.

In his daily work as Director of the Zoological Gardens in Zurich, Dr. Hediger has recorded many interesting observations. He has added others from the circus or from wild life, and rearranged and correlated these scattered observations first in his well-known *Wild Animals in Captivity* and now in his present volume.

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4

THE EFFECT OF SEXUAL STIMULATION PRIOR TO SERVICE ON THE BEHAVIOUR AND CONCEPTION RATE OF BULLS

By B. M. KERRUISH

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Introduction

In most animals mating is preceded by courtship, display and foreplay. It is reasonable to assume that the performance of these behaviour patterns serves not only to excite the sexual partner, but is also self-stimulating and so in the course of mating, sexual excitement increases in both sexes to a level at which copulation is initiated and consummated. Macirone and Walton (1938), Beach (1942) and Walton (1952, 1955) have shown that completion of the sexual act by the male depends upon two factors, the sex drive or sexual excitability of the male, and the excitatory value of the female or other sexual object. Courtship display and foreplay raise the level of sexual excitation of the normal male not only with respect to the receptive oestrous female but also with respect to less exciting sexual objects such as the "dummy" or the anoestrous "teaser" used for the collection of semen at an A.I. centre. An increase in sexual excitement also will tend to overcome those inhibitions which may be inherent in the use of the artificial vagina or other artifices employed in controlled mating and collection of semen, and will also overcome inhibitions due to mishandling the bull at mating, or to painful or inexpert use of the artificial vagina.

Milovanov & Smirnov-Ugrumov (1940) made an important study of bull sexual behaviour in terms of the "conditioned reflex" theories of I. P. Pavlov. They found that many sexual reflexes could be conditioned to external stimuli and conditioned inhibitions could be established. In order to prevent, or restore, flagging sexual activity in the bull the authors advocate the uses of a variety of sexual stimulators, changes in the environment of collection and alternation of sexual opportunity with frustration of libido. They found that the bull if not stimulated to a high level of excitability becomes somnolent and sluggish in sexual performance and the ejaculatory reflex weakened, with the result that a poor sample of semen is discharged. Since this work is not readily available to workers in this country and the conditions under which bulls are managed in Russia are different from those in England, experimental verification of this work is desirable. Rowson (1946) has stressed the care needed in handling bulls at service in A.I. centres in England, and has described individual cases of service inhibition. He gives methods of handling the bulls and of collecting semen which are designed to stimulate sexual arousal where there is diminution of sex drive. This paper clearly illustrates the necessity of providing adequate sexual arousal to initiate mounting and ejaculation, and Rowson's methods have proved very successful in reducing the number of bulls at A.I. centres which refuse to serve.

A state of inhibition which is perhaps the same as that described by Milovanov and Smirnov-Ugrumov and which leads to the "somnolent condition," is, however, more common than are the inhibitions described by Rowson, and as it can remain undetected over a considerable period, is more serious. Entire bull studs may become affected and the conception rates depressed before the condition is realised. If not diagnosed the stud may recover "spontaneously" only because of the drastic culling of the affected bulls or by fortuitous changes of routine or management.

The present paper shows that under natural conditions of free-range breeding, pre-coital sexual stimulation is much more intense than it is under conditions of controlled mating or in the routine collection of semen at an A.I. centre. An experiment with ten bulls, which were maintained for five months on a regimen of incomplete sexual stimulation and then were placed for five months on a regimen of much more sexual stimulation, shows that such treatment not only affected the sexual behaviour but significantly raised the conception rate of the bulls.

Pre-coital Sexual Stimulation in the Natural Free State

Mating in cattle on free range is a prolonged process lasting sometimes as long as 60 hours. An experienced bull running with the herd,

appears to be able to detect oestrus two or three days before its full onset. He will first single out the cow and for a day or two will keep very close to her, grazing and lying down within a few yards, and keeping her under continual surveillance. As full oestrus approaches, the male exhibits increasing interest and more intense excitement. This is sometimes shown by his licking and smelling the cow, especially round the vulva. Later, mounting is attempted but is met with repeated avoidance reactions, with consequent frustration of the bull's attempts at coitus. Finally as the climax of sexual excitement approaches and the female becomes receptive, there may be partial erection and protrusion of the penis, dribbling of accessory fluid and repeated and persistant attempts at mounting. When coitus does eventually take place it is performed quickly and the copulatory thrust is given with great vigour. The consummatory act is usually followed by fairly complete relaxation of muscular and nervous tension, until after a quiescent period sexual excitement is again built up in the performance of somewhat similar patterns of behaviour as before. In this case, however, the fully oestrous female does not make such persistent avoiding reactions and the bull's tentative attempts at coitus seem to be determined more by the temporary lowering and gradual recovery of the male drive than by lack of receptiveness on the part of the female.

During attendance on the oestrous cow, the bull exhibits excitement by giving frequent displays of masculinity, such as pawing the ground and throwing dirt over the back and withers, horning the ground, or with head lowered and nostrils distended, snorting ferociously and "threatening" any intruder, even the anoestrous cows in the herd. If other bulls are present in the same herd, the sexually excited bull reasserts his dominance by head wrestling with subordinate bulls and with horns interlocked, drives the weaker animal into submission.

The intense sexual excitement described above is built up slowly to a climax. In the early stages the bull is little aroused sexually, but by repeated stimulation through visual, olfactory and auditory receptors a highly excitable nervous and physical condition is reached by the time coitus is achieved. It is probable that the excitement which accompanies pre-coital display has an effect not only on the sexual organs but also a general effect upon body metabolism, on the level of secretion of the endocrine glands and on the vascular system, so that excitability and tone of the whole body are increased and a more vigorous, and better co-ordinated ejaculation is given at coitus.

Incomplete Pre-coital Sexual Stimulation Under Conditions of controlled Mating and Collection of Semen by Artificial Vagina

Service conditions when mating is controlled or semen collected by artificial vagina do not provide the complete sequence and the intensity of the sexual stimuli described above. If deliberate action is not taken to provide some special stimulation, serious consequences may result. The routine adopted at an A.I. Centre, to ensure smooth running and prompt delivery of semen, may itself be inimical to the arousal of sexual excitement in the bulls. Lack of opportunity to "display" and "work up" sexual excitement, and repeated use of the same old unattractive teaser cow may well tend to produce incomplete sexual stimulation. This again may cause lack of co-ordination of the neuromuscular and endocrine components which are essential to vigorous and effective ejaculation. The onset of weakened sexual performance may be gradual and is not easily recognised, as there may not be any very significant increase in the "reaction-time," and the bull's performance may appear to be satisfactory. Reaction-time is the interval between leading the bull up to the teaser cow and completion of coitus and is often taken as an adequate criterion of sexual libido and performance. Actually, reaction-time may remain constant, even when conception rate is falling, and the only indication that there is anything amiss may not be given until the figures for the conception rates become available. A typical case history is that of the bull which starts well at an A.I. Centre, mounting and thrusting with vigour and with his whole attention concentrated on service. After a variable period there may be a drop in semen quality without change in the reaction time. The bull's behaviour, however, alters. There is a more passive response to handling and the teaser is approached with apparent indifference, without erection or partial protrusion of the penis, and with no pre-coital discharge of urethral secretion. There is no keen appetitive anticipation of service, and the bull's movements appear to lack co-ordination and undivided sexual intention. On reaching the teaser the response is immediate. The cow is mounted and a fairly active thrust given into the

artificial vagina. The bull however, seldom serves close up to the cow and the ejaculatory thrust may not be given until the artificial vagina is pushed down on to the penis. (By contrast, an active bull should always serve into the artificial vagina held high up on the flank of the teaser.) After ejaculation, sexual excitement passes off immediately into the phase of post-consummatory relaxation, and the affected bull assumes a disinterested mien, may even move away from the teaser to graze, or will stand behind her with head resting on her hind quarters and eyes half closed. In some cases there is a discontented and worried air about the whole performance and after dismounting the bull shows "disapproval" by voicing short undertone moanings.

In general the condition is characterised by a lack of undivided concentration upon the sexual act, and the bull's sexual activity may be easily diverted to other activities, or inhibited by relatively slight disabilities. As examples of the first, a naturally active bull may divert his attention from the teaser to the man leading him, and play with or fight against the nose ring or leading pole, or turn to the head of the cow and attempt horn play. As examples of ease of inhibition, many bulls become acutely sensitive to serving in a confined space or near distracting objects. In these cases "fear" of colliding with walls, overhead beams or with other objects during or after service may be the immediate cause. An impatient and voluble collector may also distract and confuse a sensitive bull. Even slight pain accompanying service or collection will rapidly give rise to inhibition. There is a real dislike in some bulls for serving on a concrete surface. Mounting is undertaken with noticeable care and the thrust is timid and lacking in follow through, probably due to fear of losing balance and falling heavily on a hard surface. Such bulls may serve satisfactorily on springy turf or with a thick "gymnasium" mat under their hind feet. There are a great many other environmental factors affecting the bull's performance and care is required to detect and remove distracting or inhibiting objects. When inhibition has been firmly established in a bull, drastic treatment may have to be used. An extreme example is that of an

Table I. Extraneous Variables Likely to affect Sperm Production

Variable	Pre-experimental Period Incomplete Sexual stimulation Sept. 1953—Jan. 1954	Experimental Period Complete Sexual stimulation Feb. 1954—June 1954
Material	Same bulls used in both periods	
Ration	7 lbs. concentrates, hay and roots	
Collectors	Two well-trained collectors	One of the original collectors resigned on 1954, and was replaced by a slightly less experienced man
Interval between collections	Six to seven days sexual rest between collections	
No. of ejaculates per collection	1—3	
Semen dilution rate	1:20—1:50	
Treatment of semen	Semen cooled slowly and citrate buffer-egg yolk added at even temperature: stored at +5°C. for not longer than 3 days. Intra-uterine insemination with cervical fixation per rectum.	
Seasonal effect	Mean National conception rates for months Sept.—Jan. Sept. 69.1 Oct. 68.8 Nov. 67.7 } 66.7 Dec. 66.1 Jan. 65.3	Mean National conception rates for months Feb.—June. Feb. 64.8 Mar. 65.1 April 64.4 } 65.3 May 65.5 June 67.1

Aberdeen Angus bull which would only serve after being forced to run round a field, led by one stockman and goaded with a stick by another. On finally approaching the teaser the beating was intensified, so that when the bull did mount and serve, his act seemed motivated by an intense desire to escape punishment. It is also recorded that a Shorthorn bull which would normally only serve with much hesitation and gave unsatisfactory semen, would serve with savage and single minded vigour if first used as a teaser for other bulls to mount.

Experimental Determination of the Effect of Pre-coital Sexual Stimulation on Behaviour, Semen Production and Conception Rate

In order to determine experimentally the practical importance of complete or incomplete sexual stimulation on coital performance, ten bulls which had been for five months (September, 1953—January, 1954) on a collection routine of "incomplete sexual stimulation" were then placed for five months (February, 1954—June, 1954) on a collection routine of much intensified sexual stimulation. The behaviour and the conception rates (three months non-return rates) were recorded over both periods. In planning this experiment attention was given to the possibility of extraneous factors other than collection routine affecting the results and consequently conditions were kept as constant as possible throughout the entire ten months.

Table I shows a comparison of two periods with respect to a number of variables which were thought might possibly affect sperm production or conception rate. With the exception of the unavoidable change of collector and

Table II. Regimen of Pre-coital Sexual Stimulation and Effects on Reaction Time

Pre-experimental period of incomplete sexual stimulation, Sept., 1953—Jan., 1954.			Experimental period of complete sexual stimulation, Feb.—June, 1954.	
Bulls brought out from box individually when needed for collection and led round 2-3 times. All bulls led on pole. Collections made indoors or on concrete stance with crate fixed to wall in front.			Bulls tethered near collection site outside for 15-20 mins. before collection except in very wet weather when collection was made indoors on concrete but without fixed crate. The pole was not used where it was safe to do without. Various methods of stimulation were used according to individual bulls as set out below.	
Bull No.	Individual Treatment	Reaction Time	Individual Treatment	Reaction Time
F.1(1) F.2 F.3 F.4	Allowed to serve after leading up to teaser and turning round two or three times	Immed-iate	Tethered for 30 min. in front of teaser. Early presentation with teaser but service not allowed before 2-3 min. frustration of mounting.	No change but actions keener
G.1	Collection attempted first with teaser in crate, generally unsuccessful. Then bull allowed to follow teaser round field until he responded.	Very slow Up to 1 hr.	Early presentation with teaser. Tethered early and intensive frustration of mounting provided. Used as teaser for other bulls. Frequently led in front of teaser while other bulls were mounting.	5-10 mins. keener
G.2	As above	15-30 mins.	As above, often used as teaser prior to collection.	Immediate
G.3	Intensive stimulation (2).	Good 3-5 mins.	As above	Same 3-5 mins.
S.1	Led up to teaser in crate	Slow 10 mins.	As above—occasionally used as teaser.	Immediate
S.2	ditto.	5-15 mins.	As above—not used as teaser.	,,
S.3	ditto.	5-10 mins.	As above—not used as teaser.	,,

(1) F=Friesian. G=Guernsey S=Shorthorn.

(2) The only bull in which intensive stimulation was used during both periods was G.3 which therefore serves as a control in the experiment. This bull was put on intensive sexual stimulation on 1st Oct. on account of poor sex drive. The sexual behaviour, reaction time and conception rate (see Table III) remained unaltered throughout both the pre-experimental and experimental periods.

Table III. Effect of Pre-coital Sexual Stimulation on Conception Rates in Bulls

	Pre-experimental period of incomplete sexual stimulation, Sept., 1953—Jan., 1954										Experimental period of complete sexual stimulation, Feb., 1954—June, 1954.									
Bulls	F.1	F.2	F.3	F.4	G.1	G.2	G.3	S.1	S.2	S.3	F.1	F.2	F.3	F.4	G.1	G.2	G.3	S.1	S.2	S.3
1st paid inseminations	1178	1954	579	1155	422	632	577	502	482	576	1594	1444	999	991	393	806	381	651	648	630
3 months non-returns	673	1153	345	689	262	378	368	338	323	363	1105	973	695	644	273	551	250	473	478	435
C.R. %	57.1	59.0	59.5	59.6	62.0	59.8	66.0	67.3	67.0	63.0	69.3	67.3	69.5	70.6	69.4	68.2	65.6	72.9	73.7	69.0
	Friesian				Guernsey			Shorthorn			Friesian				Guernsey			Shorthorn		
1st (paid) inseminations	4866				1611			1560			4948				1580			1929		
3 months non-returns	2860				1008			1024			3407				1090			1388		
C.R. %	58.7				62.5			65.6			68.0				68.9			71.9		
	Total All Breeds										Total All Breeds									
1st (paid) inseminsations	8037										8457									
3 months	4892										5885									
C.R. %	60.8										69.5									
	Difference C.R. % + 8.7%																			

possible seasonal effect, extraneous factors were constant. Both the change of collector and the seasonal effect would tend to *lower* the conception rates during the experimental period.

Table II sets out in general terms the collection routines adopted in the two periods and also the individual treatment given each animal and the results on reaction-time (see p. 126).

It will be noticed that in the case of the Friesian bulls which had quick reaction-times in the pre-experimental period no change was noted in this characteristic but copulation was performed with greater vigour. In the case of the Guernseys and Shorthorns which were initially slow, improvement in the reaction times was very marked.

In Table III the conception rates are set out and the experiment is presented in graphical form in Fig. 1. From the tables and the graph it is seen that there was a very significant rise in the conception rate with increase in sexual stimulation prior to service. Since semen quality was not assessed it is not possible to say whether any qualitative or quantitative change took place in the semen other than that causing a rise in success rate. Nevertheless, the most probable explanation of the results is that the higher the level of pre-coital stimulation, the more vigorous and efficient will be the ejaculation, and a better sample of semen will be produced.

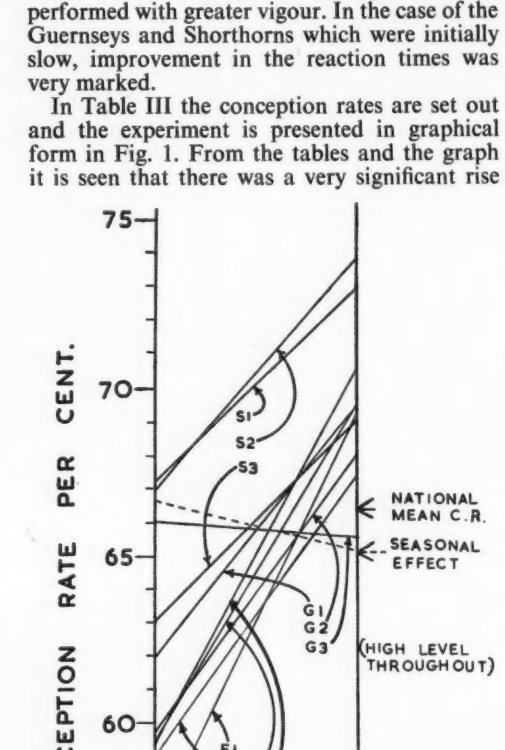

Fig. 1

Summary

At A.I. centres, and to some extent on farms where a rigid routine of controlled mating is practised, adequate sexual stimulation prior to copulation is not provided. Compared to natural free-range matings, the preliminary courtship, displays of masculinity and the rough and tumble of foreplay and temporary frustration are absent. Sex drive is consequently reduced and the vigour of the ejaculatory reflex diminished, as a result a poorer sample of semen is produced and conception rate is lowered. With lowered sex drive post-consummatory relaxation is prolonged and long periods of sexual continence are required between collections. Old bulls, of which there are many at A.I. centres, are especially affected.

When ten bulls which for at least five months had been on a sexual regimen of inadequate sexual stimulation were placed for five months on a regimen of intensive sexual stimulation prior to semen collection, there followed a marked improvement in sexual behaviour and a significant rise (8.7 per cent.) in the conception rate.

Acknowledgment

I am indebted to Dr. A. Walton, A.R.C. Unit of Reproductive Physiology and Biochemistry, Cambridge, for advice on the presentation of the data and their tabular and graphical representation.

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THE EFFECT OF SOCIAL FACILITATION ON FOOD INTAKE OF PUPPIES FED SEPARATELY AND TOGETHER FOR THE FIRST 90 DAYS OF LIFE

By W. T. JAMES and T. F. GILBERT
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A number of experiments have shown that group eating has a decided effect on food intake in puppies (Ross, S., & Ross, Jean G., 1949; Ross, S., 1949; James, W. T., 1953, 1954). Dogs eat more in groups than alone, and they are stimulated to further eating in groups after satiation in individual feeding. The question arises regarding the nature of social facilitation. It may be based on learning, or it may be a natural response relatively independent of learning. In view of the fact that many experiments have shown that early experience does have an effect on many behaviours (Beach & Jaynes, 1954), the present investigation was undertaken to observe the effect on social facilitation among puppies reared by different methods. The problem, specifically, was to determine the difference in social facilitation between groups of dogs raised together and separately for the first 90 days of life.

Method

Animals

Two groups of three Beagle-Terrier F 2 Hybrids were used in the experiment. The animals were born in the psychology laboratory at the University of Georgia.

Procedure

Group I was fed separately each day after weaning for 90 days. Group II was fed together each day after weaning for the same period. Each group was fed only once a day in the late afternoon. At the end of the 90 days food intake was measured on both groups each day for 40 days. On 20 of the days the animals of each group were fed separately, and on 20 alternate days they were fed together. The food consisted of Purina Chow mixed with warm water, with every care taken to have it the same consistency from day to day. Food intake was determined by weighing the animals on a sensitive scale before and after eating. The second weighing was not made until each animal had walked away from the pan, and had an opportunity to return for further licks if it desired to do so.

Results and Discussion

Figure 1 represents the mean grams food intake plotted as a function of both social and

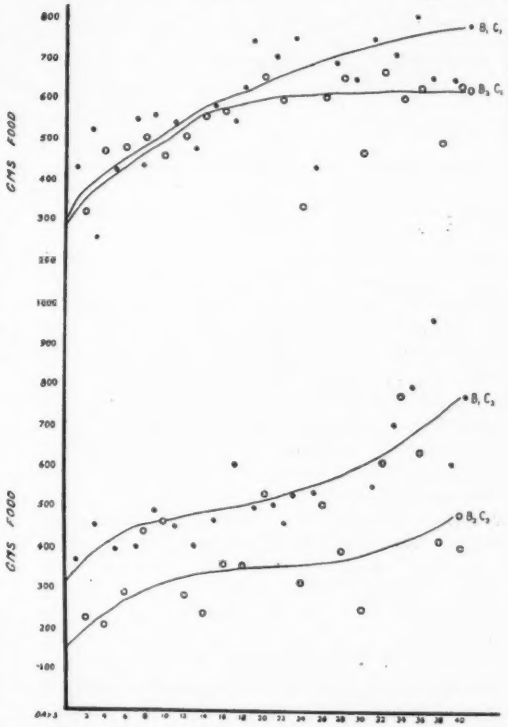

Fig. 1. The curves indicate the grams of food intake each day under conditions of social feeding (squares) and individual feeding (circles). The increase in food intake under social feeding did not begin until after 14 days in group I. (B_1. C_1. B_2. C_2.), reared in isolation. In group II, (B_1. C_2. B_2. C_2.), reared together, social facilitation was shown from the beginning of the experimental tests.

isolated feeding days during the experimental period. The upper curves (B_1-C_1.B_2C_1) presents the results for group I, and the lower curves (B_1C_2.B_2C_2.) for group II. All curves were smoothed by inspection. There is an expected systematic growth of food intake for both

Table I. Analysis of Variance of Daily Food Intake Measures

Source a	df	Mean Square	F	P
Conditions of raising (C)	1	613,374	1.6	Not significant
Between Ss treated alike	4	371,871		
Total Between Ss	5			
Days (A)	19	134,259	9.72	Less than .001
Feeding conditions (B)	1	457,016	28.23	Less than .01
AxB	19	32,923	2.82	Less than .01
BxC	1	82,028	2.07	Less than .025
AxBxC	19	26,761	2.39	Less than .01
Error within (A, AxC)	76	13,809		
Error within (B, BxC)	4	16,154		
Error within (AxB, AxBxC)	76	11,665		
Total error within	156	12,824		
Total within Ss	234			
Total	239			

groups under both feeding conditions, this merely reflecting continued growth of the animals. It is clear that group II ate more under conditions of social feeding than when fed in isolation. Effects of social feeding is not apparent in group I until about day 14, when this group begins to eat relatively more and more when fed together. This would indicate that, while social feeding produces greater intake in animals used to being together, it requires about a week of social feeding for it to become effective in the group fed in isolation during the first 90 days. The nature of the curves suggest a higher order interaction between conditions of feeding, raising and days. Table 1 is a summary of the analysis of the variance of the mean food intake measures. The main effects of raising conditions is not significant. However, this test included the measurements of the non-social feeding days which naturally should alternate meaningful differences. Also, group I and II represented different litters that were considerably different in size at the beginning of the experiment. The higher order interaction between days, feeding and raising conditions is significant at the .01 level of confidence, indicating that social faciltation has a different effect from day to day depending upon the conditions under which the animals were raised. This test supports the belief that the seemingly gradual development of social facilitation in group I as compared to the immediate appearance of facilitation in group II, is a real phenomenon. The main effects of feeding conditions is significant at the .01 level of confidence, and verifies the presence of social facilitation. Other tests are of no essential interest.

The immediate appearance of social facilitation in the control group on day 91 indicates that the lack of facilitation in the experimental group is not due to a maturation factor. Since dogs in both groups were together in every activity except feeding, this suggests that facilitation is a learned behaviour specific to the feeding situation and not generalizable from mere social contact involving other activities. The presence of other animals in the feeding situation may act as a secondary reinforcement of the behaviour. In a previous paper James (1954) has demonstrated that effectiveness of secondary cues in producing excessive amounts of instrumental food-getting behaviour where the secondary cues were behaviour of the experimenter, other animals, and sounds coincident with the operation of the apparatus. That generalization of non-feeding social activities is not at all present cannot be asserted without an additional experiment in which a third group of animals is raised in complete isolation of one another.

Summary

One group of three Beagle-Terrier F 2 Hybrids were fed separately for ninety days following weaning. On day 91 they were fed together on alternate days for nearly six weeks Social facilitation was not present during the first 14 days but gradually appeared after this. A similar control group, fed together for the first 90 days, evidenced social facilitation from

the beginning of the tests. These data suggest that learned secondary reinforcements are produced in the social feeding condition specific to the feeding situation and do not generalize from other social activities

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NOTES ON THE TERRITORIAL BEHAVIOUR OF CAPTIVE TEN-SPINED STICKLEBACKS (*Pygosteus pungitius*)

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This paper describes the establishment of territories by male and female Ten-spined Sticklebacks (*Pygosteus pungitius* L.), coincident behaviour, and the performance by females of behaviour normally considered to be characteristic of males.

Material

In April, 1955 six fish were taken from a pond near Cambridge and put into an aquarium 18in. × 7in. × 7in., furnished with *Callitriche* sp., *Elodea canadensis* and *Fontinalis antipyretica*. The fish were cryptically coloured and very small—all well under one inch in length. They were fed on abundant *Daphnia*, etc., and grew rapidly. (It is probably significant that the pond from which they came was very deficient in small animal life).

The Establishment of Territories

Of the six fish, two proved to be males and four females. Both the males and two of the females set up territories during the 35 days of observation. Although the males started to defend territory first, their aggression at its peak was no more marked than that of the females. Previous accounts have described territorial behaviour only in males*: this may have been the result of keeping the sexes separated until the males had set up territories and the females were ready to spawn. The present study shows that territorial behaviour certainly may occur in females under some conditions and suggests its presence in nature.

A summary of the sequence of events is as follows.

On day 4 after capture, the largest fish was breaking off pieces of weed root and carrying them in its mouth. This fish was now dark on the ventral side and often threatened other fish. Some green thread algae was added to the tank and this fish (hereafter called A) at once dashed into it with snatching movements of the mouth. At first the material thus gathered was carried only a short distance and dropped (cf. Sevenster, 1949; Tinbergen, 1951; and van Iersel, 1953) but later occasional mouthfuls were taken to the *Fontinalis* and left there.

By day 5 the nest was well formed and A had established claim to two-thirds of the tank. This situation continued for eight days. A's defence of territory sometimes relaxed late in the evening when other fish would be allowed to cruise freely through the tank.

On day 12, a fish operating from the far left corner of the tank threatened in response to A's attacks. This fish—B—was still one of the smallest but was beginning to show male colouration although the ventral marking was little more than a line of shadow. The other four proved to be females.

During the day B's aggressiveness to A increased and he twice chased him half way back along the tank. From day 12 to day 20 B's retaliatory behaviour continued. He extended his territory towards the front of the tank and the boundary became marked and stable at six inches from the left corner.

On day 20 the largest of the females—L—was trying to set up a territory in the midde of the tank, on the boundary between A and B, and threatening both. Since the onset of B's resistance A had made virtually no additions to his nest and the setting up of a territory by L as well indicated that there would be even less likelihood of A settling down to complete breeding behaviour. On day 21, therefore, B and the two smallest females were removed to another tank.

A at once became intensely aggressive again and although L was usually in the left corner after B's removal, she offered no resistance to A's renewed onslaughts until day 30, when she threatened him and followed him when he left. By the end of the day she bit him for the first time and her following became pursuit and even attack.

On day 31 there was conflict between L and the other female, M, who had taken up a territory in the left back corner and attacked L

*I am indebted to Dr. Desmond Morris for pointing out to me that he mentioned territorial behaviour in female Ten-spined Sticklebacks in a footnote to "Some Comments on Conflict and Thwarting in Animals," Bastock, Morris & Moynihan, (1953). *Behaviour*, **6**, 1, and for allowing me to read in manuscript his study of this species. This work is in press as a *Behaviour* Supplement and gives a detailed account of territoriality in females.

if she ventured there; the day was marked by continual combats between them.

By day 32 L became violent in her attacks on A. Although she did not seek him out, he seemed unble to keep away from her territory even though he was repeatedly attacked there: on one occasion L pinned him to the ground and bit him viciously before he could break away and flee. He spent the rest of the evening dashing wildly about the tank and next morning L was removed.

A's nest had deteriorated while he was preoccupied in conflict with B and during L's last day with him he abandoned the site and started a new nest further from L, with the entrance facing away from her. On days 33 and 34 he built here but only sporadically as the new site brought him into conflict with M. He became increasingly aggressive to M and by the end of day 35 was as violent to her as L had been to him. Since he was again having his attention distracted from building, M was removed.

B and the females were now together in one tank the same size as the first one and it might have been anticipated that conflict would arise there. Although B had been in the tank for twelve days before L was introduced and his male colouration had extended a little, no conflict had been seen. After L's arrival there were a few encounters (in which either B or L was usually involved) but these amounted to no more than mild threat. There was no sign of any preferred areas.

Nest-building

A's nest-building accorded with the description given by Sevenster (*l.c.*). After the removal of the last female he abandoned his latest site (it was somewhat insecure, on the outside edge of the *Fontinalis*) and began in the *Callitriche* at the other end of the tank (formerly B's then M's, territory). He abandoned this as well in two days and started higher up and further back. Materials used were chiefly vegetable but on several occasions he detached snail spawn from the weeds, chewing it, spitting it out and re-gathering it several times. Even when it had been placed in the nest, he would sometimes fetch it out again more than once before finally leaving it inside.

Defence of Nest Against Other Animals

A's territorial defence extended to other animals than fish. He removed a caddis case an inch long from the nest entrance, biting at the larva until it relaxed its hold and then carrying the case the length of the tank before dropping it. He similarly removed a small snail (*Planorbis* species) and also fiercely attacked a very large *Limnaea stagnalis* on the ground below the nest. This was done by repeated bites at the tentacles until the snail turned away.

Fighting Behaviour

The postures adopted by the fish in fighting followed the descriptions given by Sevenster (*l.c.*) but A's tactics in his conflict with L were interesting.

At times he came forward steadily but very slowly, stopping if L looked at him and going into reverse if she moved towards him. Alternatively he would advance in short spurts. Or again he would stay motionless about four inches from L. Facing each other, and both horizontal, the fish would then move to and fro, every forward move of L matched by a backward move by A, and vice versa—as if the fish were joined by a wire.

A twice carried out encircling movements, by the far side of the tank and so through weed cover. On the first occasion L saw him, met him as he emerged from cover, and chased him away, The second time L was not aware of his approach, having her back to him. On reaching the edge of the weeds, A shot forward, mouth open, and attacked her but she immediately recovered and chased him off.

A feature of the later stages of A's conflict with L was his rapid alternations between breeding dress and cryptic colouration. The change could be instantaneous. As A approached L he would be dark; when—but not until—he turned to flee, he became cryptic. The change was the more complete the more violently he was pursued, and would fade the more quickly if—after being chased—he went to his nest and gave it attention. At first the cryptic markings showed only on the rump which was never as densely black as the ventral parts, but on L's last evening in the tank A became so generally pale under the cryptic markings that it was difficult to recognise him. A moment later he made an attack on M and his male colours returned with violent abruptness. He then went to his nest and bored through it and emerged as dark as he had ever been. Two minutes later, worsted in yet another skirmish with L, he was again pale and cryptic.

An interesting encounter between A and M took place on one occasion. A attacked M who

was slow to evade him. He thereupon dashed at the ground and took up a mouthful of dirt and algae which he held for a moment and then spat out. This is interesting when compared to the sand-digging threat posture of the Three-spined Stickleback (*Gasterosteus aculeatus*) which was first interpreted as displacement feeding but later shown experimentally to be displacement sand-digging, and thus part of the nest-building behaviour (see Tinbergen & van Iersel, 1947). The Ten-spined normally builds its nest in weeds so that sand-digging forms no part of the nesting behaviour but this incident suggests that picking up sand is likely to occur in aggressive situations. (The presence of algae was almost certainly fortuitous since a film of the weed was scattered about on the substratum).

"Pseudo-male" Behaviour by Females

Although Morris (1952) described "pseudo-female" behaviour by frustrated males, he adds that "only one male activity has been seen to be performed by females, and that is fanning," adding that "the female is only seen to fan on rare occasions and under specifically frustrating conditions." In his experiments the sexes were not put together until ripe females were introduced at the time of spawning. In the present study other instances of "male" behaviour were seen in addition to the territorial behaviour described above. It should be emphasised that the fish involved were all females, but were not ripe at the time: L did spawn (in A's current nest) but not until 25 days after the end of the observations covered by this study.

On day 8 a female visited A's nest briefly. He saw her, came up quietly, then made a sudden attack and drove her off.

On day 13, four visits were made to A's nest, three of them certainly by the same fish. The first was short—the female merely nosed at the entrance, fanned, and left. She turned back at once and this time entered the nest for half her length. She stopped momentarily, then pushed on until her nose protruded from the exit. She lay thus for nearly a minute (cf. Morris *l.c.*). A was near but took no notice. The female pushed through the nest and left but came back within four minutes, stopping near the entrance for a moment and then leaving.

Some twenty minutes later a female which may or may not have been the same one (at that time it had not been possible to identify the females individually) came to the nest, fanned, went into the nest, paused for two or three seconds, pushed through, and left.

On day 25 (by which time the females were known one from another) L went to A's nest wriggled half way in, backed out, fanned and left. This was the last time a female was seen to visit the nest. It is noteworthy that all these visits took place before A had come into conflict with any female.

Apart from nest visiting and entering, and the fanning accompanying some visits, females were seen to thrust themselves violently into growing weeds. L did this twice (the second time after her removal to the other tank) and other females did so on several occasions.

Since none of these females was ripe and therefore presumably not frustrated, these examples of behaviour patterns normally shown by one sex appearing in the other suggest that no hard and fast line can be drawn between male and female behaviour patterns. Hinde (1955), referring to finch courtship, makes the similar point that "there is no category of behaviour which is not performed at least sometimes by both sexes" and suggests that "the nervous mechanism underlying the behaviour is probably always present in both sexes."

Acknowledgment

I should like to thank Dr. R. A. Hinde for his helpful criticism during the preparation of these notes.

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STUDIES OF FIGHTING IN CHAFFINCHES. (2) THE EFFECT ON DOMINANCE RELATIONS OF DISGUISING FEMALES AS MALES

By P. MARLER

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In a general study of the behaviour of non-reproductive Chaffinches in relation to the social hierarchy (Marler, 1955) it was found that, during fighting, both sexes responded differently to male and female opponents. Further experiments were conducted to investigate the part played by male colouration.

The female Chaffinch, *Fringilla coelebs*, is predominantly greyish brown in colour, the male differing in its blue crown and nape, chestnut mantle, and reddish-orange underparts. The latter was elected for study, as the most conspicuous difference between the sexes. Females were taken at random from captive flocks of non-reproductive birds, and their underparts were dyed with red inks in imitation of the male. Then they were placed in open-air aviaries with normal males and females, to observe the effects of the red colouration on aggressive behaviour. A peck-right hierarchy exists in winter Chaffinch flocks, with males dominant to females (Marler, 1955) and the effect of colouring on status provides a convenient index.

Seven series of experiments were conducted.

1. Normal females were matched with "red" females to determine the effect of male colouration on fighting between females.

2. The two lowest-ranking birds in two flocks of eight females, were coloured red, to see whether this affected the existing hierarchy.

3. "Red" females were matched with hand-reared females which had never seen adult males, to assess whether any effects of red colouration were the result of previous experience of males.

4. Females were placed with males dyed bright green for two weeks, and then their response to females which had also been dyed green, was observed. This series was also designed to test whether strange colouration as such has an effect on fighting.

5. Males were matched with mixed groups of "red" and normal females, to assess the response of males to coloured females.

6. Males were placed with "red" and normal females which had already been in the cage some weeks, to observe the effect of giving coloured females the advantage of prior residence.

7. Males were matched with "red" females which had been separated from males for some weeks, in an attempt to reduce any learned fear they might have of them.

Experimental Procedure

The birds were all trapped on the Ornithological Field Station at Madingley, Cambridge, with the exception of some used in Series 3 which were taken from the nest 7 to 8 days after hatching and reared by hand. All were serially marked with coloured leg-rings. The experiments ran from October to February during the period in which the gonads are regressed.

The experiments were conducted in open-air aviaries. The usual dimension was 2m. × 2m. × 2m. but in certain cases, signified in the text, a larger one 9m. × 3m. × 2.5m. was used, and in Series 3 small indoor cages, ½m. × ½m. × ½m. were used. The smaller ones were provided with single dishes for food and water and the larger with two. The food was often removed for about 30 minutes before the start of observations, when it was replaced, to increase the frequency of fights at the food dish. Observations were made from canvas hides.

A mixture of red, orange and burnt sienna waterproof inks was used for colouring the "red" females and an aqueous solution of malachite greeen for the "green" birds. The breast feathers were first moistened with a dilute soap solution to make the dyes flow on to the feathers. To ensure that the treatment had no direct effect on subsequent behaviour, controls were treated with soap solution alone in one experiment.

It is well known that previous social experience can affect the behaviour of animals during aggressive encounters (Ginsburg & Allee, 1942; Kahn, 1951). This was reduced to a minimum, as a source of error, by selecting birds to be matched, at random, from different flocks. In one case a more elaborate attempt was made to

unify previous experience (Series 4). No individual had previously encountered any of the others in the experiment except, in some cases, birds in the same class (male, "red" or normal female), and in Series 2, in which established flocks were used. The experiments were conducted in aviaries of which none of the birds had had recent experience, except in Series 6.

Results

Records are only given of those fights in which one individual was clearly victorious. The encounters were instigated in several different ways. Most frequently one bird would evict another from the food or water dish, or a perch. Occasionally a bird would approach a food dish only to be repelled by another already in occupation. The details of behaviour during these encounters and its motivation are described elsewhere (Marler, In Press). For the present purpose they are all summarised by two figures as wins or losses. A single defeat of a dominant bird by a subordinate is not treated as significant, since birds known to be subordinate may occasionally displace dominant birds accidentally. They may fly up to the food dish from the floor of the aviary while unaware that the dish is already occupied, and thus startle the feeding dominant enough to make it flee. Such occurrences are rare and, although recorded as defeats, are clearly not significant from the present point of view. Two or more counter attacks against a dominant are regarded as signs of undecided dominance relations.

Series 1. The Matching of "Red" Females wth Normal Females

In five experiments, 2 "red" females were matched with 2 normal females whose breast feathers had been treated with soap solution, to act as controls. They were placed simultaneously in small aviaries, and observed for 4 to 30 days, until a moderately stable hierarchy was formed: Some dominance inversions occurred during observation, hence the apparent irregularity of some of the hierarchies, which formed peck-right and straight-lines at any one time.

From the first moment the "red" females had an advantage (Table I). Of the 20 possible pair-contacts between "red" and normal females (4 per experiment), "red" females were completely dominant in 13, and in 2 met only slight opposition. Normal females had more wins in 3 contacts and in 2 the scores were about equal.

If the total wins and losses of "red" and normal females are compared (Table II) then the supremacy of red-breasted birds is even more emphatic. They won 84 per cent. of all encounters with normal females. Evidently birds with the male red breast have a high chance of

Table I. Series 1. The Outcome of Fights Between "Red" (underlined) and Normal Females. Reading from left to right, each horizontal row records the victories of the individual at the left hand side over the other members of the flock.

	O	BkR	G	P
O		13	7	37
BkR	12		17	21
G	14	4		21
P				

Expt. 1. (Obs. over 30 days)

	RW	RWB	GY	BkY
RW		27	15	21
RWB			11	10
GY		5		18
BkY				

Expt. 2 (Obs. over 7 days)

	R	BkY	PWP	P
R		15	8	5
BkY	15		10	14
PWP	1	1		21
P				

Expt. 3 (Obs. over 7 days)

	H	W	PWS	OW
H		10	32	27
W			19	14
PWS		4		24
OW		1		

Expt. 4 (Obs. over 6 days)

	RO	BR	OBkY	GYB
RO		15	15	11
BR	2		17	28
OBkY				18
GYB				

Expt. 5 (Obs. over 4 days)

Table II. Series 1. Summary of the Total of "Red" Female Wins against Normal Females

	Expt. No. 1	2	3	4	5	Total
"Red" wins over normal females	75	71	42	92	71	351
Normal wins over "red" females	29	11	25	5	—	70
Percentage of "red" wins of total "red" cencounters	72	87	63	95	100	84

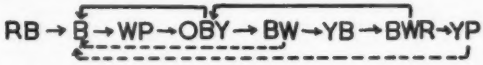
success against females not previously acquainted with them.

Series 2. The Effect of Red Colouration on the Status of the Two Lowest-Ranking Birds in a Flock

It is characteristic of a peck-right hierarchy that each member responds to others in the group during fighting, to some extent independently of their behaviour. Thus the high ranking birds in a flock have learned that they can attack the two lowest individuals—and indeed all their subordinates—with immunity. A subordinate must combat the inertia of this learned response, not present at encounters between unacquainted birds, before it can rise in status. The aim of this series was to test whether disguise with the male red breast would make this possible.

Two flocks of eight female Chaffinches were set up, one in a small and one in a large aviary. The first was observed and allowed to stablise for 25 days. On the 14th day, one bird died and was replaced (B). Therefore only the results from the 15th to the 25th day are presented here. Then the two lowest ranking birds (BWR, YP) were removed, coloured red, and replaced. Observations then continued for 16 days.

The hierarchy was moderately stable during the first period of observation after the new bird had settled down. The order may be summarised as:



The true triangular relationships are indicated by entire lines and unstable relationships with no clear dominance relations, by broken lines. B, the newly introduced bird, was the victim of these irregularities, perhaps because its position in the flock was not quite firmly established. The two birds destined for colouring—BWR and YP—had both achieved some success against higher ranking birds, but they received far more defeats in proportion to wins than any other birds in the flock (Table III).

After BWR and YP had been dyed red, the order became considerably more irregular. The "red" birds exploited fully those relationships which had previously been unstable and in addition each made a further conquest. The order thus then became

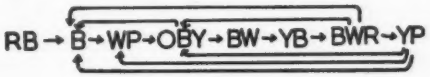


Table III. Series 2. Flock 1. The Wins of Each Individual Before and After Colouring of BW and PW, as Percentages of the Total Encounters in which each was engaged.

		RB	B	WP	OBY	BW	YB	BWR	YP
Before colouring BW	Total wins	16	35	27	21	22	28	9	4
and PW (10 days).	Total losses		15	15	10	13	33	23	53
Percentage of wins of total encounters		100	70	64	68	63	46	28	7
After colouring BW	Total wins	12	16	20	12	1	28	20	28
and PW (16 days)	Total losses		22	24	14	1	28	11	37
Percentage of wins of total encounters		100	42	46	50	50	50	65	43

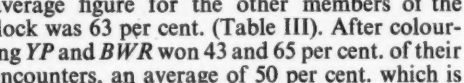
Table IV. Series 2. Flock 2. The Wins of Each Individual Before and After the Colouring of YH and GYW, as Percentages of the Total Encounters in which each was Engaged

		R	GYB	PG	OBkY	GYR	OW	YH	GYW
Before colouring the two	Total wins	37	36	23	19	23	15	18	11
lowest ranking birds.	Total losses	21	15	27	8	19	25	34	22
Percentage of wins of total		64	61	38	70	55	38	35	25
After colouring	Total wins	66	48	73	42	37	27	91	51
YH and GYW	Total losses	44	82	36	54	23	69	71	56
Percentage of wins of total		60	37	67	44	62	28	56	48

Before colouring YP and BWR gained, out of all their encounters with other birds, only 7 and 28 per cent. of wins respectively and an average figure of 15 per cent. The corresponding average figure for the other members of the flock was 63 per cent. (Table III). After colouring *YP* and *BWR* won 43 and 65 per cent. of their encounters, an average of 50 per cent. which is identical with the average figure for other members of the flock. BWR alone won a higher proportion of her encounters than all members of the flock except the despot (RB). *YP* won more than B and only 3 per cent. less than WP.

The evidence from flock 1 thus suggests that as a result of red colouration, the two lowest ranking birds had a greater chance of winning fights with dominants.

The social hierarchy in flock 2 was considerably more irregular before colouring, on the 21st day, than in flock 1 (Table V). It may be summarised as :



Once again true triangular relationships are represented by entire lines and unstable relationships by broken lines. The two lowest birds YH and GYW were involved in two of the triangles and GYW had rebelled against R, the despot; nevertheless, they had lower percentages of wins than any others in the flock (Table IV).

After their underparts had been dyed red (21st—50th day) both *YH* and *GYW* chastised their subordinates to an increased degree. The hierarchy became too complex to express clearly in a diagram, but *YH* made new conquests over GYB and OW, and *GYW* over GYB. *YH* also rebelled vigorously against R and PG. As in flock 1, most of the inversions and rebellions involved birds whose previous relationships had been unstable.

The effect of colouring is also apparent in the proportions of wins among total encounters (Table IV). Before, *YH* won 35 per cent. of its encounters, after 56 per cent. *GYW* won 25 per cent. before and 48 per cent. after. If their results are added, before colouring they won 31 per cent. of encounters, as compared with an average of 57 per cent. for the rest of the flock and after, 53 per cent. as compared with 48 per cent. for the remainder. Evidently their chances of success were considerably increased by the disguise.

Account must be taken, in these experiments, of any spontaneous tendency there may be for low-ranking birds to rise in status, during the course of time. Ginsburg & Allee (1942) anticipated this in their analysis of the effects of previous experience on social status in mice, and found the probability of a spontaneous rise to be surprisingly high. However the peck-right hierarchy of Chaffinch flocks is considerably more stable than the somewhat variable social orders occurring among mice (Uhrich, 1938; Marler, 1955) and the effect can probably be ignored.

It appears then that disguise of a female with the red breast of the male increases her chances of success in aggressive encounters, even against previously dominant individuals. But her chances are greatest against individuals whose status in the flock has previously been somewhat unstable. The behaviour of the rest of the flock towards the coloured birds, which was much more confident than towards strangers, suggested that the addition of the red breast

did not conceal their identity. However the absence of nervousness characteristic of a stranger to the flock may have played a part in this. Nevertheless in many cases dominant birds seemed to experience a conflict between tendencies to attack and avoid a "red" female they recognised as a subordinate. There are records in other species of the effects of colouring on recognition. In Ring Doves, colouring of the breast at first frightened associates, but the effect soon disappeared (Bennet, 1939). A similar result was obtained with Noddy Terns (Watson, 1908), colouring on the head producing a stronger response than on the neck, Evidently the head is particularly significant in this contest (see Nice, 1943; Guhl & Ortman, 1953), and the fact that only the ventral surface was coloured in these experiments, may partly explain the persistence of individual recognition

Series 3. The Matching of "Red" Females with Normal Hand-reared Females which had never seen Adult Males

This series was designed to ascertain whether or not the response of female Chaffinches to the red breast is conditioned. In the first part, 8 females which had been reared by hand, and which had since been in the company of other females, but had never seen adult males, were paired in small indoor cages, with wild-caught females of the same age, with red underparts. During the subsequent week observations were made on the outcomes of encounters occurring at the food dish and at other parts of the cage. In some pairs, status had not been settled by the end of the observation period and in most there was an unstable period during the first 1 or 2 days.

The "red" females were successful in 87 per cent. of their encounters with the hand-reared females (Table V). In most cases aggressive display was rare since normal females often fled precipitantly on meeting a "red" bird. In only one pair was there serious opposition by a hand-reared female and neither had achieved complete dominance after 7 days.

In four pairs the dominance of "red" birds was virtually unopposed, in three there was slight opposition and in one the birds were equally matched, with status not determined. The success of "red" birds against hand-reared females thus compares closely with their success against experienced females. However it is possible that hand-reared birds might be less aggressive than wild birds.

Another series was therefore conducted using only hand-reared birds. Of the 11 females available, 4 of those used in the previous experiment were isolated from the remainder for one month, which was probably sufficient for the two groups to forget each others' individual characteristics. These were then dyed red, placed with the others in another cage, and observed for ten days.

Eight of the 28 pair contacts between "red" and normal females were still unstable at the end of the observation period. Of the remaining 20, 16 were won by the "red" females with little or no opposition. Of the 408 encounters, "red" birds won 78 per cent. which compares favourably with the result from the previous series.

In the subsequent year 6 females were reared in complete isolation from the seventh day after hatching. At an age of about seven months three pairs were selected at random and one bird in each was coloured red. They were placed in new cages and observed during the subsequent month. "Red" females won 72 per cent. of the 141 encounters observed. In two pairs the "red" females were dominant from the start. In the third there was an extended conflict and although the "red" female was dominant at the end of the period, it won slightly fewer encounters than the normal bird (33 : 35). Nevertheless the overall success of "red" birds was very similar to that in the previous experiments.

Thus it appears that the domination of females by birds with a red breast involves a

Table V. Series 3. The Results of Fights Between "Red" Females and Hand-reared Females

	Expt. No.								Total
	1	2	3	4	5	6	7	8	
Number of wins by hand-reared females	5	1	—	—	18	7	—	7	38
Number of wins by "red" females	29	35	28	58	21	34	26	32	263

response that is not dependent on previous social experience of males.

Series 4. The Matching of Females with Green-dyed Underparts and Normal Females which had Previously been Dominated by "Green" Males

This series was designed to test whether female Chaffinches which had been dominated by green coloured males would also be dominated by green females, either because of learning, or because of a fear of strangely coloured chaffinches. In the first part, 5 females were paired in small cages with green-dyed males for fourteen days. They they were matched in outdoor aviaries, each with one of 5 green dyes females which had previously been paired with normal males, in identical conditions. They were observed for the subsequent two or three days.

In the second part, 4 groups of 3 females each were segregated in small cages, 2 groups were given 2 "green" males, and the 2 others, normal males. After fourteen to eighteen days the females with the normal males were dyed green and matched with the other females (in 6 pairs) as above. There were thus 11 paired encounters in all.

It was found that "green" females were dominant in 4 cases, and normal females in 7, an insignificant difference (Table VI). Of the total number of wins, "green" birds won 25, and normal birds 57, suggesting that in fact the abnormal birds may be at a disadvantage. Thus the attempt to condition females to submit to "green" Chaffinches failed. Also it is clear that "abnormally coloured" females have no advantage, and may be at a disadvantage.

Series 5. The Matching of "Red" Females with Mixed Groups of Normal Females and Males

The object of this series was to see whether males respond differently to "red" and normal females. It was also possible to judge whether the presence of males altered the response of normal females to "red" females.

Three groups, each comprising 2 males, 2 normal females and 2 "red" females were set up in the small outdoor aviaries, and observed for between four and nine days.

In one experiment (2) a straight line hierarchy was formed with almost no irregularities, with the order

males > "red" females > normal females.

The same basic pattern occurred in the other two flocks though somewhat marred by irregularities. In experiment 1 a "red" female—*H*—dominated both males for a brief period, before both defeated her. A normal straight-line order prevailed after this. In experiment 3 one male (W) was at first dominated by both normal females, though he later rebelled against them. With these exceptions, males dominated both "red" and normal females.

"Red" and normal females each received almost exactly 50 per cent. of male attacks, (Table VII). Thus no effect of the red breast on the frequency of male attacks is revealed.

Red-breasted females were found to dominate normal females even in the presence of males. The effect is slightly more marked than in the absence of males since "red" females won 93 per cent. of these encounters as compared with 84 per cent. in Series 1 when no males were present.

Series 6. The Introduction of Males into Established Groups of "Red" and Normal Females

The aim of this series was similar to the previous one except that the "red" and normal females were given the advantage of prior residence over the males. This is known to encourage dominance over newcomers (e.g. Schelderup-Ebbe, 1935; Braddock, 1949; Hinde, 1953). Perhaps the greater stress might reveal some difference in the response of males to normal and "red" females.

Three flocks of 2 normal and 2 "red" females were left in small aviaries for one week. Two males were then added to each and observation continued for eleven days.

Of the 12 contacts between males and "red" females, males were clearly dominant in 11 cases. In 1, a male was at first dominated by a female. Normal females were all dominated by males, the prior residence of both "red" and normal birds apparently placing the males at no

Table VI. Series 4. The Results of Fights Between "Green" and Normal Females

	Expt. No.											
	1	2	3	4	5	6	7	8	9	10	11	Total
No. of wins green females		4		7	7						7	25
No. of wins normal females	3		15			7	9	9	10	4		57

Table VII. Series 5. The Proportion of Wins by Males over Females, in which "Red" Females were the Victims

		Total wins over females	Wins over "red" females	Percentage of wins over "red" females of total over all females
Expt. 1.	Male B	66	39	59
	O	120	54	45
2.	Male GW	109	47	43
	R	53	29	55
3.	Male H	91	37	41
	W	44	28	64
	Total	483	234	48.4

disadvantage. The figures for the numbers of male wins over "red" and over normal females (Table VIII) suggest a slight but insignificant discrimination against "red" (55 per cent. of total).

There is no evidence from this or the previous series that males react in any way abnormally to females with red-dyed underparts. But it is possible that discrimination might not be revealed in the proportions of attacks. The results of Series 5 and 6 were examined to see if males attack each other more often than they attack females. From the total of 6 flocks there was an average of 21.3 attacks on each male and 17.0 on each female. The variation between experiments was considerable and the difference between these figures is not significant. Thus discrimination between "red" and normal females might not be revealed by these results.

Series 7. The Matching of Males with "Red" Females which had Previously been Isolated from Males for Some Weeks

This was a final attempt to determine whether a red breast could affect the outcome of a female's fights with males. In 2 experiments, 4 females were isolated from males for four to five weeks and then, after being coloured red, were placed in a small aviary with 4 males. After about two weeks, the "red" females were replaced by 4 normal females, which had also been isolated and thus acted as controls.

In the first experiment "red" females won 57 per cent. of their fights with males, while the control, normal females won 8 per cent. (Table IX). In the second experiment "red" females won 32 per cent. of their encounters with males, while normal control females won 7 per cent. In both cases "red" females achieved significantly more successes against males than normal females.

As well as encouraging female success against males, the red breast also affected the stability of the hierarchy to such an extent that the relationships between some males and "red" females had not been settled by the end of the observation period.

Thus a response can be evoked from males by the red breast under suitable conditions. Presumably "red" females which have had immediate previous experience of dominant males, as in Series 6 and 7, are unable to exploit the advantage that the red breast gives them over

Table VIII. Series 6. Number of Wins of Male Chaffinches over "Red" and Normal Females

		Total wins over females.	Wins over "red" females.	Percentage of wins over "red" females of total over all.
Expt. 1.	Male P	54	34	63
	Y	52	28	54
Expt. 2.	RP	26	14	54
	G	53	29	55
Expt. 3.	BY	53	33	62
	B	74	34	47
	Total	312	172	55.3

males, because they still have a learned fear of them. The presence of normal females in the cage may also have had an effect in Series 5 and 6, by enabling males to perceive by comparison that coloured females are more similar in most respects to normal females than to males.

Discussion

Female Chaffinches which are disguised with a male red breast, win more fights than uncoloured birds against both males and females. There is no reason to think that the process of colouring can have any direct effect on the aggressiveness of a female bird. Since the birds used for colouring were selected at random, half of them on the average might have been expected to be dominated by normal females. This was far from the case, for 38 out of 44 dominated their opponents. This success must be mainly a result of the response evoked in other birds by the red breast.

The outcome of every aggressive encounter is a result of mutual interaction (Carpenter, 1942), and behaviour is strongly affected by that of the opponent. In the present case it appears that the red breast first evokes an avoidance response from other Chaffinches. This in turn encourages the red-breasted female to attack, even though it might otherwise have submitted without fighting at all. A similar effect can be observed in normal fighting behaviour (Marler, In Press). With a male opponent, the effect of the "red" female's fear of him is usually to counter any avoidance response that may be evoked in him by the red breast. Only by taking special steps, which would never occur in the wild state, can male avoidance be demonstrated. But the female response must arise under natural conditions, whenever the two sexes come into conflict in winter.

The red breast of the male Chaffinch conforms with the definitions of Lorenz (1935) and Tinbergen (1948) of a "social releaser" as "a character peculiar to individuals of a given species and to which responsive releasing mechanisms of conspecific individuals react and thus set in motion definite chains of instinctive actions." It is evidently one of the ways by which Chaffinches can distinguish between the sexes.

A number of morpholical releasers involved in intersexual recognition have been described in other bird species, Noble (1936) fixed male moustaches on the face of a wild female Flicker, *Colaptes auratus* and found that her mate attacked her as though she were a rival male.

Table IX. Series 7. The Results of Encounters between Eight "Red" Females and Males as Compared with the Results with the Same Males and Normal Females

		"Red" females 1	2	3	4	Totals	Percentage wins
Expt. 1.	Wins of females against males	142	123	24	54	343	57
	Losses do.	64	69	47	79	259	
		Normal females 1	2	3	4		
	Wins of females against males	19	14	1	1	35	8
	Losses do.	115	60	88	157	420	
		"Red" females 1	2	3	4		
Expt. 2.	Wins of females against males	41	5	78	7	131	32
	Losses do.	47	75	101	61	284	
		Normal females 1	2	3	4		
	Wins of females against males	6	16	1	—	23	7
	Losses do.	30	100	98	90	318	

A male Yellowthroat, *Geothlypis trichas*, copulated with a stuffed female which was placed in his territory and attacked it when a black mask, in simulation of the male's plumage, was placed on its face (Noble & Vogt, 1935). The sexes of Shell Parakeets are distinguishable by the blue cere of the male. Males are completely deceived by a female with a blue-painted cere, which they attack, and by a male with a brown-painted cere which they court (Cinat Tomson, 1926). The chances of a Chicken's success in initial fights are increased if it is given a large false comb (Guhl & Ortman, 1953), perhaps a close parallel with the Chaffinch red breast.

In several species of sexually dichromatic lizards it has been shown that simple disguise of a female by colouring as a male will cause her to be attacked, instead of courted, by a territory-holding male. *Sceroporus undulatus* (Noble & Bradley, 1933), *Lacerta melisellensis* (Kramer 1937) and *L. viridis* (Kitzler, 1941) all behave in this way. In none of the above examples is it known whether or not the responses are learned.

Releasers by which the female can distinguish the sexes have been described in fish. The red ventral surface of the reproductive male Three-spined Stickleback, *Gasterosteus aculeatus*, is the releaser for the female's response as well as for fighting for other males (see Tinbergen, 1951) Among Cichlid fishes, in several species of *Astatotilapia* the female inherits a response to the reproductive markings of the male (Seitz, 1940). It is with these examples from fish that the Chaffinch red breast is to be placed, as a releaser involved in sexual recognition, the response to which is not acquired by conditioning.

Summary

Female Chaffinches with underparts dyed red, in imitation of the male, won the great majority of aggressive encounters with normal females, and dominated them in the social hierarchy.

The colouring with red dyes of the two lowest birds in established flocks of 8 female Chaffinches resulted in a rise in status, and an increase in the proportion of encounters won. The attacks were usually directed against birds whose previous status had been somewhat unstable.

Females which had been reared by hand, without ever seeing adult males, showed the avoidance response to females with a red breast, and were dominated by them. The response is thus not acquired as a result of social experience of males.

It was not possible to condition female Chaffinches to avoid birds with green underparts by placing them with green-coloured males and then testing them with green-coloured females. There was no avoidance of unusually coloured (i.e. green) females.

Male Chaffinches placed in the aviary at the same time as "red" and normal females did not discriminate between them in aggressive encounters, but dominated them in the usual way. In the presence of males, "red" females still dominated normal females. The same result was obtained if the females had the advantage over the males of prior residence.

If "red" females were separated from all males for four to five weeks and then matched against them, they won significantly more fights than normal females treated in the same way. Thus the red breast could evoke avoidance responses from both females and males, though they seldom became manifest in the latter, because of their greater aggressiveness.

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THE BEHAVIOUR OF EGG-LAYING WORKERS OF BUMBLEBEE COLONIES

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Introduction

In 1912 Sladen reported that bumblebee workers sometimes lay eggs when the fecundity of their queen is rapidly declining.

A number of observers have noted that egg-laying workers tend to attack one another (Sladen, 1912; Frison, 1917; Plath, 1934; Brian, 1952). In the present investigations such behaviour has been studied in detail.

Behaviour in Natural Colonies

Bumblebee colonies were collected in the field and placed in observation nest-boxes, the bees being given individually distinctive markings.

In one colony (*Bombus pratorum*) the queen attacked some of the workers, none of whom retaliated. In another colony (*Bombus agrorum*) one of the workers not only attacked several workers, but also the queen; the latter did not appear to be unduly perturbed by the attacks made upon her. In another six colonies, (one *Bombus derhamellus*, one *B. agrorum*, and four *B. pratorum*) animosity only broke out between the workers after the queen had been removed or had died. In each of these colonies one of the workers appeared to adopt the status of the queen and to be "dominant" to the others. Most of the time the dominant bee of a colony incubated a new clump of eggs which she had probably laid. She frequently butted her head, with mandibles agape, against bees that came near to the egg clump.

Behaviour in Colonies Started in Confinement

Colonies were started by confining distinctively marked workers,* with or without a queen, in nest-boxes each containing sugar syrup and a lump of pollen. Under such conditions the ovaries of many of the bees developed and eggs were usually laid within a few days.

Confinement of Workers with a Queen

In five experiments ten *B. pratorum* workers were confined with a queen who had headed another colony. In one case a worker became dominant over all the members of a colony including the queen, who usually remained in the corner of the nest-box.

Animosity was not apparent between the workers of the remaining four colonies whilst their queens were still present, although the queen of one colony was seen to attack some of them. However, in each of these colonies one of the workers became dominant within a day of the removal, and in one case of the death, of the queen. Three of the members of the colony whose queen had died repeatedly bit her body, especially around the mouth-parts.

Confinement of Workers Without a Queen

Queenless colonies were made by confining ten workers together. Usually only one bee in each colony (the dominant) attacked the others. Sometimes, however, there was another bee present (the 2nd dominant) which attacked any bee other than the dominant. Rarely, there was a third bee present which attacked any bee in its colony apart from the dominant and 2nd dominant.

The mean number of attacks which occurred in these queenless colonies during daily 15 minute periods of observation, are shown in Fig. 1.

There was a sharp rise in the mean number of attacks at the time at which the first batch of eggs was laid; thereafter the number of attacks gradually declined until, seven days later, comparatively little animosity could be seen. It seems that aggressive behaviour of the dominant bees was associated with the development of their ovaries irrespective of the actual presence of an egg clump, since a considerable number of attacks were made before any eggs had been laid. When captured foragers were provided with sugar syrup, but no pollen, their ovaries did not develop, presumably for lack of protein, and no animosity occurred.

On two occasions the workers of a colony were placed in a nest-box containing a comb (with eggs and larvae) taken from another colony. In each case the bees exhibited the same dominance order as they had shown previously in their own nest, thus indicating that the dominant bee's behaviour was not necessarily associated with the protection of eggs which she herself had laid.

On three occasions the combs built by workers were removed and on each occasion eggs were again laid within a few days. In two of these instances animosity had been apparent between the workers, and it continued at about the same level after the combs had been removed. In the third case in which no animosity had been apparent for eight days before the comb was

* Unless otherwise stated the workers were all captured foragers from *B. pratorum* colonies.

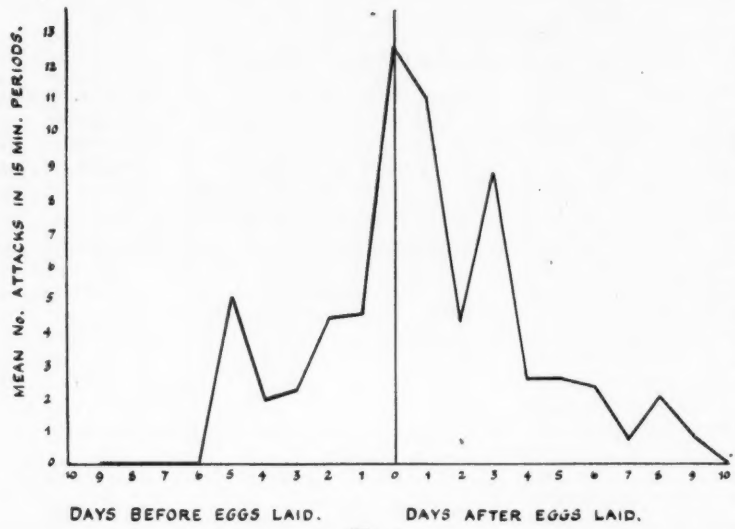
MEAN No. ATTACKS IN 15 MIN. PERIODS.
0 1 2 3 4 5 6 7 8 9 10 11 12 13
10 9 8 7 6 5 4 3 2 1 0 1 2 3 4 5 6 7 8 9 10
DAYS BEFORE EGGS LAID.
DAYS AFTER EGGS LAID.

Fig. 1

removed it failed to develop afterwards. On a further three occasions the workers of *B. pratorum* colonies, which were well past their peaks of strength and from which males and queens had emerged, were confined together. On two of the three occasions the workers laid eggs but no animosity developed.

Apparently, therefore, although there is invariably a great deal of animosity between the workers of a colony at about the time that they first lay eggs, this animosity cannot be revived even by causing them to start producing brood again.

The above data relate to bees of the species *B. pratorum*. *B. agrorum* workers were confined together on two occasions, however, and similar behaviour was observed.

Behaviour in Relation to Ovary Size

The degree of development of the ovaries of workers and queens was measured by a method similar to that used by Cumber (1949). The number of oocytes in each ovariole were counted from the point where an oocyte and trophocyte were of the same size. The mean number of oocytes per ovariole per bee is recorded as that bee's ovarian index.

In 13 of 20 queenless colonies in which the ovarian indices of the members were determined the dominant bee had the highest ovarian index, and in another colony it was equal to the highest. The dominant bees of four other colonies possessed the second highest ovarian indices, and in the remaining two colonies the third highest ovarian indices.

In four cases the bees which were attacked the greatest number of times by the dominant bees of their colonies possessed ovaries which were more, or as well, developed as those of the dominant bees concerned. In a further eight cases they possessed the second highest ovarian indices in their colonies, in two cases the third highest, in three cases the fourth highest, and in the remaining three cases the fifth highest ovarian indices.

It is apparent that in many instances the dominant bees and the bees they attacked the most possessed the most highly developed and second most highly developed ovaries respectively.

Exceptions did occur, however, so it is apparent that the assumption of the dominant status by a particular bee is not solely dependent upon the degree of development of her ovaries. No correlation was found between the size of a bee and its dominance status; indeed in 10 of the 20 colonies the dominant bee was less than the mean size of the bees present.

Change of Dominance Order in Colonies

In three colonies which were started by workers, and were not interfered with by the removal or addition of bees, changes in the dominance order occurred.

During the few days immediately before a bee became dominant she tended to be attacked by the current dominant individual significantly more frequently than the other members of the colony. (Mean No. attacks 9.4:2.2 $P < 0.001$).

It appears probable that such changes in dominance order were associated with the development of the ovaries and the laying of eggs by the new dominant bee. In one case the new dominant bee was seen to lay eggs; in another the change of dominance order occurred the day before the previously dominant bee died.

A change of dominance order may also

perhaps be associated with regression of the ovaries of a previously dominant bee, as bees whose ovaries had ceased to develop were found in several colonies. In such cases the parts of the egg tubes nearest to the oviducts, which usually contain the largest and most developed oocytes and trophocytes, contained only small yellow bodies, whilst the parts of the egg tubes nearest to the terminal filament contained oocytes and trophocytes which were not as well defined as usual.

The Introduction of Dominant Bees to Strange Colonies

On 13 occasions the dominant bee of one colony was placed in another colony. The introduced bee and the colony's own dominant bee always attacked eacth other. During the first 15 minutes after introduction the dominant bees of the colonies attacked the introduced bees a mean of 5.8 times compared with a mean of only 0.7 attacks which they made on each of the members of their own colony, whilst the introduced bees attacked the dominant bees a mean of 4.7 times compared with the mean of 0.8 attacks they made on each of the other bees.

Only on two occasions did the introduced bee initiate an attack. On the other occasions either the dominant bee of the colony attacked the introduced bee (nine cases) or some of the other bees attacked her (two cases). In most cases the introduced dominant bee was attacked only by the dominant bee of the colony concerned. The two dominant bees usually attacked each other viciously at first, but within a few minutes one achieved dominance over the other.

On five of the 13 occasions when a dominant bee was introduced to a strange colony she became the dominant bee of that colony. On the remaining eight occasions she was dominated by the dominant bee already present. On two occasions after the introduced dominant bee (A) had been dominated in the strange colony she was returned to her own and the dominant bee (B) of the colony to which she had been introduced was also added. In one case in which the two dominant bees were simultaneously placed in the colony the same dominance order continued; in the other case bee (A) was returned to her own colony first and bee (B) was introduced 15 minutes later. Bee (A) became dominant at first although later in the day bee (B) re-established her dominance.

Eleven of the dominant bees which had been introduced to other colonies were subsequently returned to their own. In nine of these colonies a new dominance order had been established in the absence of their original dominant bees. The bees which assumed dominance in these cases tended to be those which had received most attacks from the dominant bees before they were removed. (Mean of 12.7 attacks compared with a mean of 3.3 attacks made on each of the other bees of the colonies. $P. < 0.001$).

On the nine occasions on which the formerly dominant bees were returned to their own colonies in which new dominants had appeared, the first attacks were made by the newly dominant bees. The subsequent behaviour of the previously dominant bees appeared to depend on whether they had been dominant in the strange colonies to which they had been introduced. Of five bees which had been dominant in strange colonies, four were also dominant when returned to their own, but one was dominated. This latter bee had only recently become dominant in her own colony. Four bees which had been dominated whilst in strange colonies were also dominated on return to their own.

The Behaviour of Dominant Bees

In the vast majority of the conflicts which were observed between worker bees (2,071 out of 2,126) the attacking bee butted her head, with mandibles open, against her adversary. On 75 occasions on which the parts of the body attacked were noted, the attack was made upon the thorax in 52 cases, upon the head in 18 cases, and upon the abdomen in five cases.

Attacks varied greatly in ferocity. Sometimes the dominant bee pursued her adversary, constantly butting her, until she had chased her from the comb. A dominant bee rarely bit her adversary, and only if her dominance was disputed. Occasionally a dominant bee opened her mandibles when another bee approached but made no attack.

Sometimes the attacks were extremely violent; the dominant bee straddled the body of her adversary as though to sting her, but never did so. This type of attack was observed 55 times, usually between rivals for dominance, and it occurred most often either when a dominant bee was introduced to a strange colony (18 attacks) or when a previously dominant bee was returned to her own colony (20 attacks). On two occasions bees which had very recently laid eggs attacked in this way.

The dominant bee of a colony tended to remain on the upper part of the brood clump and other members of the colony tended to

avoid contact with her. Often a dominant bee attacked a second dominant bee when they met on a part of the comb in which there were no eggs, and appeared to be able to recognise the 2nd dominant bee although the latter did not seem to behave differently from the other bees in the colony.

When a dominant bee was introduced to another colony she usually climbed onto the comb, but if she failed to establish dominance she generally left the comb. Sometimes when an introduced dominant bee was attacked she lay huddled up with her abdomenal segments contracted. Within about 24 hours, however, the behaviour of the introduced bee became indistinguishable from that of the other bees, although the dominant bee usually continued to attack her more often.

Some of the bees were observed to vibrate their wings for 2-4 secs. at a time, and occasionally continued to do so for nearly a minute. The significance of this "fanning" behaviour* was not appreciated until over half of the observations had been made, comparatively few data were obtained. The number of times that the different members of a colony were seen to "fan" is shown in Table 1. Considering that there were about eight or nine bees in each colony at the time of these observations, it is apparent that the proportion of the dominant and second dominant bees which "fanned" was much higher than that of the remaining bees in the colony. In comparison with the remaining bees a relatively high proportion of dominant bees ($P < 0.001$) "fanned" when a dominant bee from another colony was first introduced, or when a change in the dominance order had very recently occurred.

* Bumblebees normally ventilate their nests by fanning.

Table I. Fanning Behaviour

Category of bee	Number of bees observed to fan	Number of times fanning occurred	Number of times fanning occurred when status of dominant bee was being disputed	Number of times fanning occurred when status of dominant bee was NOT being disputed
Dominant	17	81	72	9
2nd dominant	11	23	10	13
Other bees	30	54	15	39
Introduced dominant	4	14	14	0

The Introduction of Queens to Queenless Colonies

On twelve occasions a queen was introduced to a queenless colony (on four of these occasions she was being returned to her own colony).

Four of the queens were introduced to colonies in which no animosity had been apparent for some days, and they climbed onto the combs without being attacked. One of them, although she was not molested, attacked some of the workers directly she had been introduced and one other attacked some of the workers the next day.

In each of the other eight cases one or more of the workers present attacked the introduced queen; the dominant worker always being one of the attackers. Four of the queens immediately retaliated, but two did not do so that day but attacked some of the workers the next day. Another queen had also obviously established her dominant status by the second day although she was not seen to attack any of the workers. Only one of the eight queens which were attacked failed to become dominant; she was vigorously attacked by eight bees on return to her own colony and did not retaliate.

Queens, like dominant workers, may loose their dominant status in a colony. Thus some of the workers of one colony attacked their previously dominant queen whenever she climbed onto the comb. The next day she had an injured leg and was trying to escape from the nest-box, and two days later she was dead. The previously dominant queen of another colony remained away from the comb of her colony and the next day she too was dead.

The behaviour patterns exhibited by queens were similar to those of workers. The greatest number of (68) "butting" attacks which were observed during a single 15 minute period was

made by a queen which had just laid eggs. On six occasions queens seized worker bees as though to sting them but did not actually do so. Often when queens were introduced to colonies they appeared to take little notice of the attacks which the workers made upon them and did not necessarily move away from an attacker. Queens sometimes "fanned" their wings in the manner described above.

Discussion and Conclusions

It is well established [literature reviewed by Plath (1923) and Free (1955a)] that *Bombus lapidarius* and *Bombus terrestris* workers sometimes attempt to eat eggs at the time that male and queen producing eggs are laid in their colonies, and that the laying queens attempt to protect them. Such egg-eating behaviour was not observed during the current investigations, on the contrary, workers sometimes helped to close cells in which dominant bees had just laid eggs. Usually, however, the dominant bees would not allow other bees near them. Whenever an egg cell was opened by the author the workers quickly closed it without damaging the eggs. Only when eggs were dropped onto a comb did the workers sometimes eat them. Therefore, it is unlikely that the aggressive behaviour of a dominant bee can be explained by the necessity to protect her eggs. Indeed before such dominant workers had oviposited they frequently attacked other bees.

Pardi (1948) reported that a linear hierarchy based on dominance often exists amongst the members of a colony of Polistes wasps, such an hierarchy being similar to the social hierarchies in some vertebrate groups [work reviewed by Collias (1944), and Allee (1951)]. In the great majority of the contacts between two wasps of the same colony, one behaved as the dominant and the other as the dominated.

From the results of the present work it is apparent that a hierarchial order may also exist in bumblebee colonies, but not such a well marked one as in colonies of Polistes, as in bumblebee colonies only one or two and never more than three bees attack their fellow members. Whereas aggressive behaviour occurs continually in Polistes colonies it declined in bumblebee colonies until little or no animosity was apparent.

In queenless bumblebee colonies, as in those of Polistes, a dominant worker attacks the individual immediately below her in the social scale more frequently than she attacks one lower down in the scale. The individual most frequently attacked by the dominant worker succeeds her if the dominant bee is removed. A dominant bumblebee may lose her social status, although this probably never occurs in the case of a queen until shortly before the break up of the colony.

Pardi (1948) found that one of the factors influencing the outcome of a hierarchial contest is whether or not a wasp is in her own nest. Although in conflicts observed between two dominant bumblebee workers the individual who was in her own nest was more often victorious, this factor was not significant. Usually when queens were introduced to queenless colonies they became dominant. Their much larger size, compared with that of the workers may have helped them to do so.

Pardi (1948) found that male Polistes were dominated by workers. During the present investigations many male bumblebees emerged in the colonies but the workers were never seen to attack them nor did the males avoid the workers. In both worker bumblebees and Polistes, however, a relationship existed between the degree of development of an individual's ovaries and her position in the hierarchy, and the most dominant individual in a colony generally possessed the most developed ovaries. It appears possible therefore that the behaviour of an individual is governed to a great extent by a secretion from her ovaries, which varies in amount with their degree of activity. However, it has been shown that the results of the previous conflicts may also determine a bee's behaviour and consequently her social status.

Pardi (1948) classified the contacts between two wasps into five categories based on the behaviour of the dominant and dominated wasp. In the three categories in which the dominant wasp behaved in her most hostile manner, she struck the dominated with her antennae, bit her, or bit and seized her. The dominated wasp then either adopted a position of akinesis or offered food to the dominant. Occasionally *B. pratorum* workers, which had been severely attacked by a dominant bee, also assumed an akinetic condition.

The behaviour of a dominant individual often gives it a trophic advantage. Allee (1951) reported that low ranking birds tend to feed after the high ranking birds of their flock have fed. The behaviour of dominant Polistes induces other individuals to feed them and thus they obtain adequate nourishment for egg production. The behaviour of dominant bumble-

bees is not associated to any extent with the acquisition of food except in so far as they tend to remain in their nests and are not so active as foragers. However, on four occasions Brian (1952) observed a house-bee (*B. agrorum*) attack a forager who thereupon regurgitated a drop of nectar. The same behaviour by a *B. pratorum* worker was once seen by the author.

Extensive transmission of food (Ribbands 1953) and of "queen substance" (Butler 1954) occurs in a honeybee colony. When a honeybee solicits food she opens her mandibles, extends her tongue and moves her head towards the head of the other bee who often regurgitates food between her mandibles. This behaviour may have evolved from the offering of food by a dominated individual to its attacker, as occurs in the less organised groups of social insects. Indeed Butler & Free (1952) found that submissive honeybee intruders regurgitated drops of fluid when examined by guards. Recently Sakagami (1954) reported that in a dequeened honeybee colony aggressive behaviour develops amongst the workers about the time that the first eggs laid by the workers appear. He found that the behaviour patterns of the attacker-attacked relationship were similar to those of the guard-intruder relationship described by Butler & Free (1952) and that the attacked bee frequently offered food to the attacker.

It is apparent that at least the first and second dominant bees of a bumblebee colony were individually known to one another and probably also to the other bees of the colony. The sense of smell is generally highly developed in insects (Wigglesworth, 1954) and it seems most likely therefore that individuals are recognised by their distinctive body odours. Possibly the scent of an individual bumblebee or Polistes is associated in some way with the degree of development of her ovaries.

It is probable that in the case of such social insects as bumblebees and Polistes, which form small colonies, the behaviour of the queen or the dominant worker reduces the tendency of the majority of the workers to lay eggs. Such behaviour may, therefore, be a contributory factor in the maintenance of stability, and of an efficient division of labour, in bumblebee colonies (Free, 1955b). A social order based on active dominance and individual recognition would be unlikely to occur in social insects which form colonies of several thousands of individuals, and Sakagami (1954) concluded that no definite dominance-subordination hierarchy exists in honeybee colonies. Instead the queen honeybee produces on the surface of her body a substance which is distributed amongst the worker bees of her colony and enables them to recognise her presence (Butler 1954). There is some evidence that this "queen substance" also prevents the ovaries of workers developing (Butler 1955). It is possible that "queen substance" has been derived from a distinctive scented substance produced by the ovaries of dominant insects in more primitive social groups.

Summary

1. A social order, based on dominance, has been found to exist in bumblebee colonies.

2. In bumblebee colonies which were deprived of their queen animosity was observed to break out between the workers. Similar behaviour occurred in colonies which had been started in the laboratory by confining workers together with an abundant supply of food.

3. In each colony one of the workers became the dominant worker and attacked any of the other workers, although as many as three workers in one colony were seen to attack other bees. In most of these attacks the dominant bee butted her head, with mandibles agape, against the body of her adversary, but in more extreme instances she bit or grappled with her adversary. The number of attacks was greatest at the time that the social order was established and thereafter declined until little or no animosity was apparent.

4. In the majority of colonies the dominant bee had the most developed ovaries. The bee she attacked the most tended to have the next most developed ovaries.

5. It is thought that the dominant and second dominant bees of a bumblebee colony recognise each other by their individual scents which may be associated with the degree of development of their ovaries.

6. In practically every case in which a queen, who had headed a colony, was introduced to a queenless colony, she soon established herself as the dominant bee of the colony concerned.

7. It is suggested that the behaviour of a dominant queen or worker reduces the tendency of the majority of the other workers in a colony to lay eggs and so is a contributory factor in the maintenance of colony stability and of an efficient division of labour.

8. The extensive food transmission which occurs between honeybees may have arisen

from the offering of food by an attacked individual to its attacker such as occurs in colonies of some of the more primitive social insects.

9. The substance produced on the body surface of a queen honeybee which enables the worker bees to recognise her presence is possibly related to the distinctive scents produced by dominant individuals of less organised social groups.

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BEHAVIOUR AS A MEANS OF IDENTIFYING TWO CLOSELY-ALLIED SPECIES OF GALL MIDGES

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Introduction

The value of experiments in supplementing the use of morphological characters for the identification of closely related species of gall midges (Cecidomyidae) has recently been emphasised (Barnes, 1953). By this means several species, exhibiting only slight morphological differences and erected chiefly on the basis of possessing different host plants, have been shown to be synonymous. For example, *Contarinia torquens* de Meijere and *C. geisenheyneri* Rübsaamen have been proved (Barnes, 1950; Bovien & Knudsen, 1950) to be synonymous with *C. nasturtii* Kieffer. Later *C. isatidis* Rübsaamen and *C. ruderalis* Kieffer were added to the synonymy of *C. nasturtii* (Stokes, 1953). This present paper shows how, in contrast, experiments may confirm the validity of species.

It is unusual to find two species of gall midges in the same genus having distinct host plant ranges within the same plant genus. However, such is the case with *Dasyneura violae* F. Loew and *D. affinis* Kieffer,* both of which are recorded from the genus *Viola*, the former usually on pansy-like species and causing very hairy galls and the latter on violet-like species, making glabrous galls. Rübsaamen (1899) stated that *D. affinis* was identical to *D. violae* and when discussing this he gave examples where a single species of midge caused more than one type of gall. Later on he revised this view (Rübsaamen & Hedicke, 1925-39), but the question of their synonymity was raised again by Barnes (1948).

This paper describes observations and experiments made to test the validity of these two species, specimens of which were also examined in a study of possible variable characters.

* The pale orange larvae of *D. violae* were first described (F. Loew, 1880) from rosette-like leaf galls with a thick growth of hair on *Viola tricolor* L. The midges emerged in July, August and September and were described as having 2+12 antennal segments, the flagellar segments possessing one whorl of hairs in the female and two in the male. *D. affinis* (Kieffer, 1886) was described from *V. reichenbachiana* Jord. (syn. *V. silvestris* Lamk.) and the larvae, at first whitish, then pale orange, were found living in leaf bunches, rotted leaves and deformed flowers from June to November. The midges emerged in July from galls collected in June. The female only was described, and had 2 + 13 antennal segments, the flagellar ones with two whorls of hairs.

Later collectors of galls apparently maintained the two species, separating them on the character of the galls. *D. violae* was said to cause abnormally hairy galls on *V. tricolor* L., *V. tricolor* L. var. *hortensis* DC., *V. arvensis* Murray, *V. polychroma* Kerner and *V. canina* L.; while *D. affinis* produced glabrous galls on *V. reichenbachiana* Jord., *V. alba* Besser, *V. hirta* L., *V. lutea* Huds. (syn. *V. lutea* Smith), *V. odorata* L., *V. riviniana* Rchb. and *V. canina* L. Later, hairy galls on certain varieties of violets were also ascribed to *D. affinis*. The authorities for these records and an account of the midges are given by Barnes (1948).

Methods

Galled leaves of *V. odorata* containing larvae and pupae of *D. affinis* were found in England and Holland and were placed in cages in an unheated insectary. On emergence of the midges, some were caught alive for use in experiments and others were preserved for later examination. *D. violae* was similarly reared from galls on *V. arvensis* (syn. *V. tricolor* var. *arvensis*), kindly sent from the Netherlands by Prof. W. M. Docters van Leeuwen.

For the host plant trials, which were carried out on potted plants, a number of *Viola* species was grown in an open, unheated glasshouse, using a single plant species per pot. A muslin cage was placed over each pot to prevent accidental infestation and to confine the midges which were used in each experiment. No more than six females, and often only one, was placed in any pot. The behaviour of the midges, which when mated live about one day, was watched through a hole in the muslin which was afterwards closed with cotton wool; mating and oviposition could be seen and the development of the galls was noted. On emergence, the midges of the new generation were caught daily and preserved.

Attempts were made to intermate *D. affinis* and *D. violae* by placing a male and a female of each species together in a small glass specimen tube with a cotton wool bung.

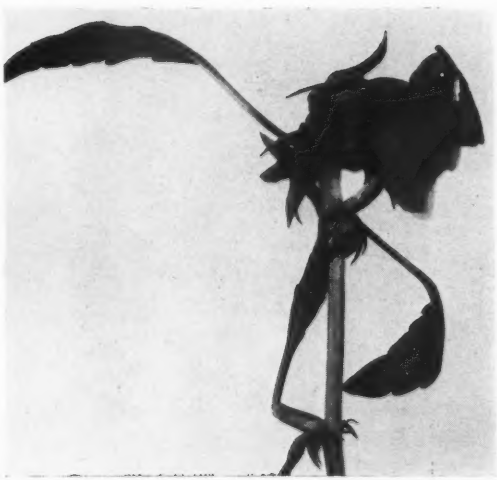
PLATE I.

(a)

Fig. 1. Galls of *Dasyneura violae* on:
(a) *Viola tricolor* (wild pansy).
(b) and (c) *V. tricolor* var. *hortensis* (garden pansy), showing (i) healthy leaf, and (ii) leaves of gall.

(b)

(i) (ii)



(c)

Host Plant Experiments

Using *V. odorata* as the host plant, midges were bred successfully in twelve out of twenty-one experiments with *D. affinis*, while galls were suspected in five others; however, there were no results in five similar experiments with *D. violae*. In contrast, no offspring of *D. affinis* emerged from fifteen experiments involving *V. tricolor* and its varieties (egg-laying was seen on one occasion on the stems of *V. tricolor* var. *nigra* and a possible gall developed on one plant of *V. tricolor* var. *hortensis* without further result), although *D. violae* produced offspring in three out of four experiments with *V. tricolor* (and oviposition on the fourth plant, which died soon afterwards) and two out of three experiments with *V. tricolor* var. *hortensis* (and galls on the third one when it died).

Thus neither *D. affinis* nor *D. violae* developed on the usual host of the other. Furthermore, it was noticed that fertilised females of *D. violae* would not stay on the plants but flew to the top and sides of the cages, whereas when caged with *V. tricolor* and its variety egg-laying began very soon afterwards.

Life Histories

The life history of *D. affinis* bred on *V. odorata* in these experiments agreed in general with that described by Barnes (1948). The length of time from oviposition to the emergence of the first imago in nine experiments set up during May and June, 1950, varied from 43-58 days.

The life history of *D. violae* agreed with the general picture given by F. Loew (1880), and the midges took from 29-36 days to develop from the egg to the adult stage.

Mating Behaviour and Experiments

Before mating, females of *D. violae* rested on the plants or the sides of the cages and extended their long ovipositors in an outward curve. The males were more active; they made frequent short flights and approached the females with quivering antennae. Each female mated only once, the process lasting one minute or less, and immediately afterwards the ovipositor was withdrawn. Oviposition began within a few hours. The ovipositor was again extruded, but this time it curved inwards and frequent small movements suggested that it was used to test leaf surfaces and stems for suitable places for oviposition. This behaviour corresponds with that of *D. affinis* described and figured by Couderc (1933).

Tests were made to see if specimens of *D. affinis* and *D. violae* would cross-mate. In five tests the females used were *D. violae*. On one occasion mating did appear to take place, and the female was then caged with *V. odorata*, but no galls developed so presumably fertile mating had not taken place. In another test the male seemed to be excited by the presence of the female, but no mating took place during three hours' observation, whereas normally the midges mate in a matter of minutes, as, for example, when *D. affinis* from England was mated with *D. affinis* reared from galls collected in Holland.

Galls

Pilosity, or otherwise, of the galls was used to distinguish between the midges in previous records, but the method could be misleading. The galls of *D. affinis* on *V. odorata* were not always glabrous. In experiments they were hard, rolled leaf galls of the type figured by Barnes (1948). Galls of *D. affinis* on *V. reichenbachiana* are shown by Rübsaamen & Hedicke (1925-39), and galls produced by *D. violae* on *V. tricolor* are also shown. In experiments the galls on *V. tricolor* could be recognised eleven days after oviposition and were harder and more hairy than normal shoots and leaves. The petioles were very short, often almost non-existant, so the leaves were bunched. Sometimes a flower developed without a stem among the galled leaves; in other cases the flower itself was deformed. Occasionally a normal flower and stem grew up away from the gall (Plate I).

Morphological Similarity of the Midges

The original descriptions of the midges gave the number of antennal segments as 2 + 12 (2 basal and 12 flagellar segments) for *D. violae* and 2 + 13 for *D. affinis*. However, variation in the number of segments is not uncommon in certain gall midge genera, including *Dasyneura* (Barnes, 1932). The numbers differ among individuals of the same parentage and may be greater on one antenna than on the other (expressed as $2 + \{^{13}_{12}\}$), or two or more segments may be imperfectly differentiated to form a larger one (expressed as 2 + 11 + big) on both or only one antenna.

After microscope examination of the *Viola* midges had shown them to be very similar in all respects*, the antennal segments were

* In the original description of *D. violae* only one whorl of hairs on the flagellar segments was mentioned, but in the specimens examined there were two whorls of hairs. Since the midges are very fragile it is probable that an error in the original description on this point was due to damage in handling the specimen.

counted. The antennae of 42 males and 80 females of *D. violae*, and 75 males and 101 females of *D. affinis* were examined; the results, which are shown in Table 1, reveal no specific difference.

Table I. The Number of Antennal Segments in *D. violae* and *D. affinis*

	2+{13 / 13+1 small	2 + 13	2+{13 / 11 + big	2+11+big	2 +{13 / 12	2+12	2 +{12 / 11
♂ *D. violae*	0	42 (9)*	0	0	0	0	0
♂ *D. affinis*	2	71 (14)	1	0	0	1	0
♀ *D. violae*	0	67 (13)	4	3	1	5	0
♀ *D. affinis*	0	81	4	2	4	9	1

* Figures in brackets indicate the number of specimens in which one antenna was broken.

In addition, one abnormal female of *D. violae* occurred with the flagellar segments 6 and 7 fused, while in *D. affinis* the following abnormalities were found : fusion occurring in the 10th and 11th, 4th and 5th, 3rd and 4th, and 10th to the 13th flagellar segments in four different males respectively. Two females were found with segments 8 and 9 fused in each, two with 10 and 11 fused and one with 7 and 8.

Discussion

Midges of the two species appeared to be morphologically identical, varying within the same range in the number of antennal segments. (If only a few specimens were examined descriptions of these species would almost certainly be misleading). The closeness of their relationship is also shown in their similar biology and possibly in the one occasion when an attempted cross-mating was seen; nevertheless, they remained quite distinct in their behaviour towards different species of *Viola*, for in experiments *D. violae* bred on *V. tricolor* and one of its varieties but not on *V. odorata*, while *D. affinis* bred on *V. odorata* but not on *V. tricolor* or its varieties, nor on *V. arvensis*.

No particular significance is attached to the fact that some females oviposited on plants outside their normal range, for some midges oviposit anywhere when in unfavourable circumstances, but the failure of larvae to establish themselves may be taken to show that such plants are not suitable as hosts. The distinct host plant range is probably a reflection of fundamental differences within the genus *Viola*.*

Whether in the course of evolution these midges will change in their host plant relationships or in morphological development is a matter for speculation. Meanwhile although the systematist may prefer to regard them as biological races of a single species the biologist will find it is more convenient to maintain them as two species.

Summary

Two gall midge species, *D. violae* F. Loew and *D. affinis* Kieffer, although morphologically identical, were found to be quite distinct in their host plant ranges within the genus *Viola*. In experiments, *D. violae*, reared from galls on *V. arvensis*, was successfully bred on *V. tricolor* and its variety *hortensis*, but would not breed on *V. odorata*; whereas *D. affinis* was bred on purple and white varieties of *V. odorata* but not on *V. tricolor*, its varieties *nigra* and *hortensis*, nor on *V. arvensis*.

The following host plants of *D. violae* are also given in the literature : *V. polychroma* Kerner and *V. canina* L.; and of *D. affinis*: *V. reichenbachiana*, *V. alba*, *V. hirta*, *V. lutea*, *V. riviniana* and *V. canina*. Further biological tests are necessary before these can be confirmed.

* This genus can be divided into groups according to chromosome numbers (Darlington & Janaki Ammal, 1945) and the midges appear to be restricted to plants in certain groups. The host plants of *D. affinis* belong to the group where the basic chromosome number is ($x=10$), while those of *D. viola* are in other groups, i.e. *V. tricolor* ($x=13$) and *V. arvensis* ($x_2=17\,(6+11)$. Two exceptions occur: *V. lutea* Huds. ($x=13$) has been given as a host plant of *D. affinis* and *V. canina* L. ($x=10$) has been recorded as a host for both midges. As the midges are indistinguishable *per se* it is possible that in these two instances mistakes have been made in identification. The only way to resolve the problem is by further biological experiments.

Acknowledgments

I would like to thank Dr. H. F. Barnes for advice and criticism in the preparation of this paper, and Mr. E. F. Warburg for information about the nomenclature of *Viola* species.

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THE USE OF RADIOACTIVE TANTALUM IN STUDIES OF THE BEHAVIOUR OF SMALL CRAWLING INSECTS ON PLANTS

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For studies of their dispersal or behaviour insects may be marked with a radioisotope supplied in the food (P^{32} is frequently used); the insects are liberated and their rates of dispersal and distances travelled are then estimated from recaptures. This subject has been reviewed by Jenkins & Hassett (1950), Lindquist (1952) and Hinton (1954).

A few workers have studied the detailed movements of individual insects tagged with a radioisotope emitting a high gamma radiation. This method is of interest to workers on insect behaviour because insects which are not visible in dense vegetation or in the soil, can easily be located, even at night. Tomes & Brian (1946) and Brian (1947) attached metal foil labels 2 mm. in diameter containing radium sulphate to elaterid beetles; they studied the insects' movements in grass and on the surface of the soil. Arnason, Fuller & Spinks (1950) and Fuller, Spinks, Arnason & McDonald (1951) attached Co^{60} wire to elaterid larvae and to cutworms to study their movements in soil. Jenkins & Hassett (1950) reported that Zr^{95} had been injected into cockroaches for tracking the insects. Banks (1954) used the radium labels of Tomes & Brian to follow the movements of late stage larvae of *Coccinellidae* on bean plants in the field; these labels were, however, too large to use on first instar coccinellid larvae (length 1.5—2.0 mm.); the methods now described for the latter could be readily adapted for other small crawling insects.

For studies of the behaviour of the unfed newly-hatched larvae on plants, the radioactive material had to be suitable for external application as small labels, yet have a sufficiently high specific activity for easy detection with a Geiger-Müller counter from about one foot away. Radioactive tantalum (Ta^{182}) met these requirements; the metal can be obtained readily as fine strip or wire, and it emits a high gamma radiation; it has a half-life of 120 days and the target element (Ta^{180}) can be quickly irradiated to a suitable activity.

Preparation of Labels

Tantalum metal, as strip 0.05 mm. × 0.16 mm. cross section, was irradiated at the Atomic Energy Research Establishment, Harwell, to the required specific activity. Two levels were used, see below.

Small pieces were cut off with a knife from the irradiated strip which was held under water by a glass slide; the pieces of metal were then collected with a pipette and mounted in glycerine jelly on microscope slides.

The average dimensions of the labels were 0.05 mm. × 0.16 mm. × 0.23 mm. (volume approximately 0.002 c mm.) and their weight was approximately 0.03 mg.

Attaching the Labels to Larvae

It was essential to immobilize the insect so that the label could be attached quickly and accurately with a small spot of adhesive; and to ensure the safe transfer of the label from the glycerine jelly before the adhesive dried. In preliminary experiments, larvae kept still by chilling recovered too quickly for the easy attachment of labels; the use of anaesthetic was considered undesirable. An apparatus was devised to overcome these difficulties.

The apparatus, of aluminium, consisted of a slide running from side to side in the grooves of a rectangular base plate fitted over the foot of a low power binocular microscope (Fig. 1).

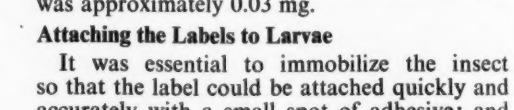

Fig. 1. Plan of the apparatus used in labelling coccinellid larvae. a—metal slide running in grooves of base plate b; c—adjustable stop for slide; d—fixed end of hair which passes over larva and under the plasticine e; f—microscope slide with tantalum label under the microscope whose foot, g, is shown.

The larvae to be labelled was held still under a hair stretched across the metal slide to the left of the operator; on his right was the microscope slide with the tantalum label in glycerine jelly.

One end of the hair was fixed to the metal slide by sticky tape; the other end passed beneath a lump of plasticine which, when pressed backwards or forwards, altered the tension on the hair. The fixed end of the hair was raised slightly above the surface of the slide.

The larva was placed on the slide under the hair with a brush and the hair drawn lightly across it. This operation was best done with the naked eye but further tension on the hair could be applied under the microscope by moving the plasticine.

With the larva securely in position and under the microscope, a stop on the base plate of the apparatus was adjusted to ensure that it could be still slid away and returned to the same place. Then the metal slide was moved to the left bringing under the microscope the tantalum label which was removed from the jelly on the point of a needle. The operator kept his eye on the label while he moved the slide to the right, bringing the larva again into view; the label was then placed on the slide near the larva.

A small spot of seccotine having been dabbed on the prothorax of the insect with a needle, the label was immediately picked up with the same needle and transferred to the glue on the insect. (Any delay in doing this was troublesome, because a film soon formed on the spot of glue, making it difficult to remove the needle from the larva which would then be dragged from under the hair.) Finally, a spot of water-colour paint was smeared over the seccotine; the paint protected the drying glue and allowed the observer to distinguish labelled larvae from others marked with different colours.

On larger larvae, cellulose paints were used as adhesives, instead of seccotine; the somewhat larger quantities of paint then used did not dry so rapidly as the very small spots required for first instar larvae.

Some Effects of Labelling

First stage larvae of several species of Coccinellidae were labelled with *un*-irradiated metal and all cast their skins normally in the usual time; the spots of glue and paint on the thorax did not interfere with ecdysis. Labelling raised the mean weight of first instar larvae of *Coccinella 7-punctata* L. from 0.155 mg. to 0.192 mg., an increase of approximately 24 per cent.; nevertheless, larvae moved actively, attacked aphids readily and behaved apparently in the same way as unlabelled larvae.

Labels of two levels of radioactivity were used to investigte effects of radiation on growth and behaviour. Labels with an average initial specific activity of 7.5μc (250 μc/mg.) produced marked adverse effects: newly-laid eggs surrounding a label did not hatch although controls from the same batch developed normally; first instar larvae became less and less active, ceased feeding and after two or three days died without casting their skins; two larvae underwent a partial ecdysis and developed malformations of the thorax immediately below the labels. Late stage larvae were apparently not affected by the labels and continued their growth normally, but because of the harmful effects on the young larvae, the use of labels of this activity was discontinued.

Labels with a lower specific activity (1.3 μc. per label or 42 μc/mg.) had no noticeable effects on growth or behaviour. Hatching occurred at the usual time; first instars and all other larval stages carrying the labels moved actively, attacked aphids readily and cast their skins successfully at normal times. These labels were satisfactory for the study of movements of coccinellid larvae of all stages; marked insects in clumps of beans or on potato plants were readily detected from a distance of about one foot with a portable Geiger-Müller counter of the type described by Godfrey (1954).

Acknowledgments

I am indebted to my colleague, Mr. H. L. Nixon, for his advice on the use of radioisotopes, and to Murex Ltd., Rainham, Essex, for a gift of tantalum strip.

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BOOK REVIEWS

Psychology as the Study of Behaviour. An Inaugural Lecture. By O. L. ZANGWILL, Cambridge University Press. 1954. Pp. 36. 2s. 6d.

In an inaugural lecture a professor is expected to review the general position of his subject to discuss the history of the department of which he is taking charge, and also to indicate the lines of development which he thinks profitable. All these tasks Professor Zangwill accomplishes with grace and fairness. Those who have been colleagues of both will especially appreciate his warm tributes to Sir Frederic Bartlett. The lecture touches on many aspects of "psychology," whether human or animal; but it is, of course, with the latter that we are mainly concerned here.

Zangwill regards psychology and physiology as "broadly co-extensive" but "it is convenient to treat physiology as the study of individual organs, and psychology as the study of the organism when it operates as a unit or whole." He wishes to see the study of behaviour linked even more closely to that of the nervous system, and refers especially to Hughlings Jackson, Sherrington, Head, Rivers, Franz and Lashley, and Beach as pioneers.

This emphasis on neurology will be questioned by some students of behaviour. Bechterev, Pavlov, and J. B. Watson are duly appreciated in their historical settings; but the "flourishing school of Neo-Behaviourists" (which has sprung mainly from the work of C. L. Hull and B. F. Skinner) receives some acid strictures. They "have thrown out not merely the mind but the brain as well," and Zangwill "views with some concern the prevalent tendency in American psychology to set up behaviour study as a wholly independent department of science." Zangwill clearly thinks of the brain as a sounder foundation for future studies than the current "formidable array of intervening variables and hypothetical constructs." All this raises the very wide question of whether students of behaviour should formulate hypotheses before there is any direct physiological method of studying underlying mechanisms.

Lashley and Hull have shown the merits of their very different methods. No one interested in the present position of behaviour study can afford to neglect Professor Zangwill's survey.

G.C.G.

Avian Physiology. By PAUL D. STURKIE. London: Ballière, Tindall & Cox. 1954. Pp. viii + 423. 48s.

Modern interest in the mechanisms of bird behaviour has underlined the need for an authoritative survey of avian physiology. This book is the first attempt to summarise existing knowledge on this subject. It is primarily intended for "teachers, students and research workers in poultry science and husbandry and in veterinary medicine" and mainly describes work with the fowl, duck and pigeon. It will certainly prove a useful reference source for workers on the behaviour of birds, but it has serious though largely unavoidable shortcomings in this respect. There is no chapter on the nervous system and only a cursory consideration is given to special senses. On the other hand the sections on reproduction and the endocrines, which occupy nearly half the text, are extremely well done. The remaining sections deal with circulation, respiration, thermoregulation, digestion and metabolism.

The book is a somewhat uneasy mixture of student text and advanced treatise. Thus, for example, on page one we are told that "Blood contains a fluid portion (the plasma), salts and other chemical constituents, and certain formed elements, the corpuscles . . ."; while on page eighty seven that "Acute thiamine deficiency in pigeons results in sinus arrhythmia, bradycardia, and A-V block.." Useful though by no means complete bibliographies are given at the end of each chapter. The book is written in simple English and pleasingly printed on glossy paper. The many figures are of a high standard and there are numerous informative tables and experimental protocols.

B.A.C.

The Natural Regulation of Animal Numbers. By D. LACK. Oxford University Press. 1954. Pp. 343, 52 text figures. 35s.

Under natural conditions the population sizes of most animals vary within limits which are very restricted compared with those their potential rate of increase could allow. Dr. Lack here seeks to elucidate the controlling factors. He starts from A. J. Nicholson's thesis that the relative stability of population size is due to a dynamic balance—the farther the numbers rise or fall, the greater the tendency to return to the previous level. It must thus depend on density-

dependent factors influencing either the reproductive rate or the mortality: the former must be smaller or the latter greater at high densities than at low.

Evidence is provided for the view that clutch or litter size has been adapted in each species so that the maximum number of young are reared: in the Swift, for instance, large clutches may produce fewer young than small clutches in bad weather because the parent cannot provide enough food. Fecundity falls slightly with population density in some species, but this is probably not an important effect in birds, though it may be in some other groups (e.g., deer).

Although density-dependent mortality factors must be important in nature there is little direct evidence about their action. The relative importance of food shortage, disease and predators varies between different groups of animals: amongst birds food is probably the most important.

Dr. Lack then applies these basic principles to the study of population cycles and irruptions, and to the significance of migration, gregariousness and dispersion. The greater part of the discussion and of the extensive bibliography (*c.* 1,000 references) is concerned with birds, but the more important literature relating to other groups is summarised. The author describes his book not as a textbook, but a signpost, and his original views on many previously controversial issues will certainly point the way for further advances. The discussion is always vivid and stimulating, and ecologists will certainly come to regard the book as a classic. It is important that it should also be read by students of animal behaviour, for ecology and behaviour study cannot be divorced: either alone is ultimately non-viable.

R.A.H.

The Distemper Complex. By LEON F. WHITNEY and GEORGE D. WHITNEY. Orange, Connecticut: Practical Science Publishing Co. 1953. Pp. viii + 219. $ 5.00.

This work has arisen out of the senior author's *Canine Distemper and the Diseases of the Distemper Complex*, which in turn was based upon an elaboration of a series of articles contributed to a dog magazine. It is meritable therefore, that despite its 1,500 references this "History, symptoms, diagnosis, pathology and treatment of eleven of the diseases which comprise the distemper complex" differs considerably in style from a conventional veterinary textbook, consisting in many parts of somewhat pithy abstracts. It nevertheless represents a useful aggregation of information and as such is likely to be widely read by veterinarians.

A critical discussion of the subject matter is clearly out of place in this journal, but one lesson to be learned is the importance of close clinical observation. Readers of the *Bulletin of Animal Behaviour* will recall the pleas that were made for the application of behavioural studies to clinical veterinary science, and any study of the group that Whitney and Whitney have discussed collectively must support that attitude.

A.N.W.

The Seals and the Curragh. By R. M. LOCKLEY. London: J. M. Dent. 1954. Pp. vii + 149. 15s.

The sub-title of this popular work is "Introducing the Natural History of the Grey Seal in the North Atlantic," and it is clear from the text, which is accompanied by several good photographs, that the author has many original observations that are worth putting on scientific record alongside the material acknowledged under "Bibliographical Notes" on p. 143. Unfortunately for the serious reader, however, this volume is clearly aimed at a much wider public and is therefore a mixture of record and narrative. It is sincerely to be hoped that a scientific paper will follow.

A.N.W.

Bird Pageant. Field studies of some East Anglian breeding birds. By A. W. P. ROBERTSON. London: Blatchworth. 1954. Pp. 192. 21s.

This book on the birds of East Anglia, seen against evocative descriptions of their habitats, is an example of amateur natural history at its best. It surveys the characteristic birds of the area, all from personal observation, and deals in detail with the Montague's Harrier, Crossbill Woodlark, Stone Curlew, Hawfinch, Wryneck, Corn Bunting and Moorhen. There are many new and interesting facts about their behaviour, carefully recorded, yet unencumbered by the boring (to anyone but the specialist) lists of vital statistics that sometimes mar works of this kind. Of the two rather incompatible tendencies, to observe the whole behaviour, and to count things, Commander Robertson has advisedly concentrated on the former.

P.M.

The Waterfowl of the World, Vol. I. By JEAN DELACOUR. Illustrated by Peter Scott. London: Country Life. 1954. Pp. 284, colour plates, 33 maps. £5 5s.

Their beauty, economic importance and amenability to captivity have long given the Anatidae a particular interest for ornithologists. Further, since they form a distinctively characterised and relatively homogeneous group, they have provided excellent material for taxonomic studies.

This book, covering the whistling ducks, swans, geese and shelduck, is the first of three volumes which attempt to "provide a synthesis of all that is known of the waterfowl of the world." Under the headings of "characteristics," "distribution," "general habits" and "captivity" a vast amount of information is summarised for each species and sub-species. To achieve a balance between such different aspects of the life of each species which would satisfy every reader would of course be impossible; this reviewer would have liked more emphasis on behaviour in nature than in captivity, and more detailed descriptions of courtship and aggressive displays; but there can be no doubt about the magnitude of the author's achievement in making this synthesis. This book, following in the best tradition of the great ornithological monographs, and written and illustrated by two such acknowledged experts on wildfowl, cannot fail to become a classic work of reference. It is a pity that so many will find it beyond the reach of their pockets.

R.A.H.

Birds of the World. By PAUL BARRUEL. London: Harrap. 1954. Pp. 204, 16 coloured plates and many photographs. 60s.

In summarising existing knowledge about the lives and habits of birds in 200 pages, Paul Barruel has achieved much within limits which prohibit a profound review. The text, which reveals a broad and up-to-date knowledge of ornithological literature (though the bibliography is limited to a few dozen titles), is designed for "as wide a public as possible, sportsmen as well as naturalists." It is centred round the c. 200 photographs, selected from the work of many different individuals and nearly all first class. There are also 16 over-vivid coloured plates which, together with the lavish production, will carry the book beyond the pockets of a high proportion of those it was intended to reach.

R.A.H.

Sea Birds. By JAMES FISHER & R. M. LOCKLEY. London: Collins. 1954. Pp. 320, 9 coloured and 68 black and white photographs, 66 maps and diagrams. 25s.

The authors describe this New Naturalist volume as "a statement of some of the facts concerning the wonderful sea birds of the North Atlantic." Their extensive field experience enables them to deal with many aspects of their subject—evolution, distribution, populations, movements and behaviour; and to discuss the birds group by group—petrels, pelicans, skuas, gulls, terns and auks. Most of the book is excellent—full of facts, but clearly and entertainingly written, and well illustrated. The distribution maps are especially to be recommended: each is drawn on a projection chosen as being particularly suitable for the range of the species in question.

Unfortunately, from the point of view of this journal, the standard of the sections on behaviour falls sadly below the rest of the book. There are frequent unjustified generalisations about groups of birds of which only one or two species have so far been studied; in several places tentative surmises or unproven theories (such as the "Fraser Darling effect") are represented as established fact. This is a pity, for the book as a whole gives a good picture of the biology of sea birds.

R.A.H.

Wild Animals in Captivity. By H. HEDIGER. London: Butterworths Scientific Publications. 1950. Pp. ix + 207. 30 illustrations. 35s.

Dr. Hediger's book is one which should be noticed in this journal, even though it was already well known in this country when received for review. The author, who is Director of the Basle Zoo, writes about the keeping of animals from a biological point of view. To give but one example of his recommendations, Dr. Hediger is convinced that "the captive wild animal is, as a rule, under occupied, under exercised and over cared for," and stresses the importance for continued health of training in biologically suitable tasks; this can fill the role of occupational therapy in our own species.

Addressed primarily to zoo staffs, this book will nevertheless provide every zoo visitor with a new view of the animals he sees. Although the author often fails to follow up the full implications of his observations, their variety and minutely detailed character abundantly demonstrate the breadth of his experience.

R.A.H.

The Dancing Bees. By KARL VON FRISCH. London: Methuen. 1954. Pp. 183. 16s.

Professor Karl von Frisch has written this book about honeybees for the layman; it contains the interesting part of the subject without the ballast of practical instruction that a handbook must provide or the comprehensiveness of a learned book.

The English title might imply that the book is solely concerned with communication between bees, but in fact the book is a translation of the fifth edition of *Aus dem Leben der Bienen*, and the original title is a more accurate description of the contents. The book commences with a simple description of the bee colony, and goes on to tell of life within the colony, of the senses of bees, of how they find their way about, and of their dance language. The latter section occupies less than one-quarter of this well-balanced book.

The original German version first appeared thirty years ago, and recent discoveries have not always been incorporated in the revisions, e.g., the account of division of labour is based on the work of Rosch (1926) and not on that of Lindauer (1952). This is not an important criticism of a work which is designed for the general public as an introduction to the subject; for them it is made additionally interesting because honeybee activities are compared (always legitimately) with those of humans and of other living creatures.

The book is well written, and it has been carefully translated by Dr. Dora Ilse; the fact that it is recommended by the Book Society is sufficient indication of the quality of its prose; it is the most desirable introduction to this fascinating subject.

C.R.R.

Practical Taxidermy. By JOHN W. MOYER. Pp 146, numerous photographs and diagrams. New York: Ronald Press Co. $3.

This book gives a clear and concise account of the taxidermy of all groups of vertebrates. It covers every stage, from collecting in the field to the final mounting, and a particularly helpful chapter on the preparation of solutions is included. The illustrations are excellent, whether photographic or diagramatic, and make the text abundantly clear.

G.E.D.

BOOKS RECEIVED

The following books have been received, and in appropriate cases will be reviewed as space permits in early issues.

H. Hediger (1955)
Studies of the Psychology and Behaviour of Captive Animals in Zoos and Circuses
London: Butterworths Scientific Publications. 30s.

Konrad Z. Lorenz (1954)
Man Meets Dog
London: Methuen & Co. 15s.

G. V. T. Matthews (1955)
Bird Navigation
Cambridge University Press. 12s. 6d.

A. F. Demaine (1955)
The Roller Canary
London: Cage Birds. 3s. 6d.

J. H. P. Brymer (1954)
Guide to Tropical Fishkeeping
London: Water Life. 35s.

A. W. Schorger (1955)
The Passenger Pigeon, its Natural History and Extinction
Madison: The University of Wisconsin Press. $7.50

J. W. Reid (1955)
Pigs
London: Farmer and Stockbreeder Publications Ltd., E. & F. N. Spon, Ltd. 18s.

H. G. Andrewartha & L. C. Birch
The Distribution and Abundance of Animals
Chicago: The University of Chicago Press £5 12s. 6d.

J. A. Laing (1955)
Fertility and Infertility in the Domestic Animals
London: Baillière, Tindall & Cox 35s.

John Hammond, Ed. (1955)
Progress in the Physiology of Farm Animals (*Volume* 2)
London: Butterworth Scientific Publications. 45s.

C. W. Emmens (1953)
Keeping and Breeding Aquarium Fishes
New York: Academic Press Inc.

John B. Bonner (1955)
Cells and Societies
Oxford University Press. 25s.

Karl Plath, Malcom Davis, Cessa Feyerabend & Irving E. Altman (1955)
Parrots Exclusively
Wisconsin: All-Pets Books, Inc. $1.25

E. L. Moon (1955)
Experiences with my Cockatiel.
Wisconsin: All Pets Inc. $2.00

ANIMAL BREEDING ABSTRACTS

This journal covers the world's published research on breeds, breeding, productivity, growth, genetics and reproduction of all farm livestock, poultry, fur bearers and other animals of economic importance, as well as the small laboratory animals. The subject of the review article in Volume 23 No. 3 (September) is "Hereditary Factors Affecting Reproductive Efficiency in Cattle", by D. H. L. Rollinson.

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The Journal of the British Trust for Ornithology

Edited by H. N. SOUTHERN

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